THE ROLE OF SEED AND SEEDLING PREDATORS, AND BROWSERS IN
THE REGENERATION OF TWO FOREST CANOPY SPECIES (*MIMUSOPS
BAGSHAWEI* AND *STROMBOSIA SCHEFFLERI*) IN KIBALE FOREST
RESERVE, UGANDA

By

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This dissertation is dedicated to my late mother Eve
Marjorie Mugerwa and my father Paul Stephen Mugerwa
without whose support and guidance I would not have
achieved this much.

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Much of the world's terrestrial biodiversity is
concentrated in tropical rain forests, but tropical rain
forests constitute a mere 15% of the earth's surface. Given
the paucity of these ecosystems, and the economic pressure
to exploit them, efficient management practices in forests
that are not protected against exploitation are needed to
ensure long-term survival of all species. Selective timber
harvesting is among the possible sustainable uses of
tropical forests; however, it can only be sustained if it
ensures efficient regeneration, which depends on survival of
seeds and seedlings. It is therefore important to assess
seed, seedling and juvenile tree survival in logged forests
to suggest future management plans that encourage
regeneration.

In this study (July 1992 through June 1993), the impact
of seed and seedling predators on *Mimusops* and *Strombosia*

regeneration was investigated in mature and logged forest parts of Kibale Forest, Western Uganda. Rodents were the major cause of seed and seedling mortality. Rodents were, however, more abundant during this study than in past studies in Kibale, and, unlike in past studies, rodents were more abundant in the mature than logged forest. When rodents were excluded, seedling establishment of *Strombosia* was equally high in gaps and understory of mature and logged forests. In the mature forest, more seeds of *Mimusops* established as seedlings in gaps than understory when rodents were excluded.

In control experiments, seed survival between gaps and understory was unpredictable. Results were influenced by seed species and forest type. However, positive correlations between seed survival and litter depth, and negative correlations between seed survival and ground vegetation cover were observed. Therefore, examinations of seed removal should also incorporate subtle site differences, such as litter depth and ground vegetation cover.

Apparently, recruitment of *Mimusops* and *Strombosia* into adult size in disturbed forests is retarded by elephant browsing. Elephants selected saplings and poles size trees of *Mimusops* and *Strombosia*. Furthermore, stem damage on both species was more common in the logged and logged-and-treated forest than in the mature forest.

CHAPTER 1

INTRODUCTION

Tropical rain forests constitute only 7% - 15% of the earth's surface, but they contain about 50% - 90% of all plant and animal species (Myers 1984, WRI 1992). Despite their paucity, and their importance for the conservation of biodiversity, tropical forests are being degraded or lost at alarming rates (Myers 1984, Struhsaker 1987). Estimates of forest conversion have, however, not been precise, ranging from 50,000 to 300,000 Km^2 per year (Sommer 1976, Bolin 1977, Wong 1978, Woodwell et al. 1978, Myers 1979, 1980 a, b, Sagan et al. 1979, Huguet 1983, Kangas 1990). The world's tropical rain forests are situated in developing countries where population growth is highest. Therefore, the future of tropical forests is uncertain because economic pressures to exploit them is likely to increase with population growth (Skorupa 1988); hence there is an urgent need to formulate forest management practices that are compatible with long-term forest conservation.

Field studies of tree regeneration in natural canopy gaps have demonstrated that seedlings and saplings existing prior to gap formation contribute greatly to the regeneration of the gap (Whitmore 1978, Brokaw 1985, Uhl & Buschbacher 1985, Uhl et al. 1991). This is one of the

primary reasons why selective timber harvesting is preferred to forest conversion. If such harvesting is carefully done, it should create gap sizes similar to those caused by natural tree-falls, that are suitable for forest regeneration (Uhl 1982, Uhl and Buschbacher 1985, Uhl et al. 1991). Unfortunately, in the manner it is typically conducted, selective logging is close to clear cutting, and may be unsustainable (Fox 1968, 1976, Johns 1983 a, b). Furthermore, systems devised to ensure sustainable use of tropical forests (de Graaf 1986, Plumptre & Earl 1986, Jonkers 1987) have tended to be ecologically unrealistic and largely unsuccessful. They tend to equate the balance between timber volumes harvested and diameter increments to being sustainable and pay little or no attention to the biological functioning of the ecosystems. In a country like Uganda, with only 5,000 Km^2 of tropical rain forest remaining (Tabor et al. 1990), it is important to pay attention to processes that interfere with regeneration of logged forests, if logging is to be sustainable. Because so little tropical forest remains in Uganda, much of it should be protected from exploitation, but this means that we should manage the non-inviolate forests even more efficiently.

Foraging by rodents and elephants will be considered here because earlier studies have indicated they influence forest regeneration subsequent to selective logging. Intensive selective logging increases rodent abundance and

species diversity (Isabirye-Basuta 1979, Kasenene 1984, Isabirye-Basuta & Kasenene 1987, Muganga 1979). Rodents consume considerable amounts of seeds and seedlings of forest trees (Janzen 1969, 1971, Harper 1977, Isabirye-Basuta 1979, Howe & Richter 1982, Kasenene 1984, Denslow 1987). Because selective logging reduces the abundance of seed producing trees, any increase in rodent population (seed and seedling predators) may have serious negative impacts on tree regeneration in logged forests.

Elephants browse more frequently in secondary forests than in mature forests (Wing & Buss 1970, Laws et al. 1975, Short 1983, Merz 1986, Kasenene 1987, Prins & Reitsma 1989, Nummelin 1990, Barnes et al. 1991). In addition to selecting secondary forests, elephants also selectively feed on specific tree species within the forest (Wing & Buss 1970, Kasenene 1984). Consequently, elephants may retard tree regeneration in logged forests. It is therefore imperative that management plans for sustainable timber harvesting in tropical forests take animal activity into consideration. It is important to assess the impact of animal species on tree regeneration in logged forests, and where possible, suggest remedies and make recommendations for future forest management.

Study Objectives

The objectives of this study were, first, to examine seed and seedling survival of two large-seeded canopy tree

species *Mimusops bagshawei* S. Moore (Sapotaceae) and *Strombosia scheffleri* Engl. (Olacaceae) in mature and logged forests; second, to examine seed and seedling survival in gaps and understories of mature and logged forests; thirdly, to determine the impacts of rodents and larger mammals on seed survival, and fourth, to compare the impact of elephant browsing on *Mimusops* and *Strombosia* recruitment between mature and logged forests.

Review of Seed and Seedling Ecology

Forest trees have been divided into two categories, gap specialists (pioneers) and canopy specialists (climax species), according to the environment in which their seeds germinate. Pioneer species typically produce abundant small seeds that can remain dormant in the soil of intact forest canopy but germinate when exposed to light, such as when a canopy gap is created (Bazzaz and Pickett 1980, Denslow 1980, 1987, Denslow et al. 1990, Brokaw 1985). Small seed size is believed to confer protection against predators, and to promote longevity at moisture levels as low as 4% (Gelmond 1978). Low moisture levels render seeds of pioneers more resistant to pathogens, and hence they can remain dormant for long periods (Gelmond 1978).

Small seeded plants generally grow in large gaps where ratios of red light to far red light and temperatures are high (Bazzaz and Pickett 1985, Fetcher et al. 1985, Denslow

1990) and their germination is typically epigeal (Ng 1978).
Epigeal germination is advantageous in that cotyledons serve
as photosynthetic organs before the seedling develops its
first pair of leaves (Garwood 1983). Furthermore, there is
little endosperm in small seeds; therefore the cotyledons
are less likely to attract seed/seedling predators (Ng
1978).

In contrast to pioneers (small-seeded trees), seeds of
climax forest tree species do not have prolonged dormancy
(Ng 1978, Bazzaz and Pickett 1980). They germinate shortly
after they are detached from their parents, or they are lost
to pathogens and seed predators (Bazzaz and Pickett 1980).
Germination of large seeds occurs in response to rainfall
rather than light (Augspurger 1979, Garwood 1983, Foster and
Janson 1985, Fetcher et al. 1985, Sork 1985, Denslow 1987).
Because they cannot be incorporated in the soil seed bank,
large seeded species can be easily driven to extinction by
logging (Ng 1978).

Large seeds have certain advantages over small seeds
(Denslow 1987, 1988, Howe and Richter 1982, Foster 1987).
Seedlings from large seeds are large, and have large amounts
of stored food. Hence, they can persist for long periods
under conditions unsuitable for photosynthesis, and are able
to recover from insect damage (Denslow 1987, 1988, Howe and
Richter 1982, Foster 1987).

Large seeds are, however, more vulnerable to seed
predators than small seeds (Janzen, 1969, 1971, Haper 1977,

Howe & Richter 1982, Denslow 1987). The large food stores that enable seedlings to survive in shades also attract animals such as insects and small mammals that forage on the forest floor (Denslow 1987). On Barro Colorado Island, predation of *Dipteryx panamensis* seeds exceeded 90% (De Steven and Putz 1984). It should, however, be noted that the authors were unable to distinguish between seed predation and secondary dispersal. Consequently, seed predation may have been overestimated. In French Guiana, seed and seedling predation of *Moronobea coccinea* and *Virola michlii* by rodents were observed (Forget 1991). In addition to eating seeds, rodents also uprooted seedlings of *Moronobea* and ate the cotyledons. In a Malaysian tropical rain forest, Turner (1990) observed predation on seeds of *Shorea curtisii* by rodents. At Las Tuxtlas, Mexico, 59% of seeds dispersed by howler monkeys were removed by rodents within 24 hours Estrada and Coates-Estrada (1991). Only 12% of *Scheelea* palm seeds survived rodent attack (Bradford and Smith 1977). These studies indicate that rodents are major causes of seed and seedling mortality in many tropical forests. The impact of rodents on seed and seedling survival, and hence, on forest regeneration, is likely to be greater in the logged forest where seed abundance is low and rodent populations are high.

Strategies of Minimizing Seed Predation in Large Seeded Trees

Large seeds are predominantly contained in fleshy and or juicy fruits that attract dispersers. The escape hypothesis (Howe and Smallwood 1982) proposed independently by Janzen (1970) and Connell (1971) suggests that seeds and seedlings beneath parent plants would suffer disproportionately higher mortality than those further away from the parents. In accordance with the escape hypothesis, predation was highest nearest to parent trees, and seedling survival increased with distance from adult conspecific trees on Barro Colorado Island (Hubbell and Foster 1986). At La Selva, Costa Rica, survival of *Welfia georgii* seeds was higher 10 m away than below a fruiting tree of the same species (Schupp and Frost 1989). For *Virola surinamensis* in Panama, Howe at al. (1985) demonstrated a clear increase of seed and seedling survival with distance from the parent.

Other studies, however, do not show such clear-cut results. Schupp (1988 a) working on *Faramea occidentalis* in Panama found that distance from the parent increased seed but not seedling survival. Distance from parent trees did not increase survival of *Faramea* seedlings in a site with high density of adult trees (Schupp 1988 b). Augspurger (1984) used seeds of nine forest tree species to test the escape hypothesis. Results from all but one species (*Ceiba pentandra*) supported the hypothesis for at least one month of growth. Nonetheless, within 12 months, most of the seedlings had succumbed to pathogens (Augspurger 1984).

Seeds of *Dipteryx panamensis* placed at least 50 m from the
parent tree at Barro Colorado Island did not have a greater
chance of survival than those beneath the parent tree (De
Steven and Putz 1984). Therefore, seed and seedling
survival is not only influenced by distance form the parent
or density of seeds and seedlings, as implied by the escape
hypothesis (Howe et al. 1985), but also by other biotic and
abiotic factors.

Building on the escape hypothesis, Hartshorn (1978)
predicted that seed survival in gaps would be higher than in
the understory because seeds in gaps are unlikely to be
beneath an adult conspecific, where mortality is high
(Schupp & Frost 1989). In this prediction, higher survival
was attributed to isolation alone. However, differences in
biotic and abiotic characteristics between gaps and
understory such as ground vegetation cover and rodent
density (Schupp 1988a) may also influence seed and seedling
survival, and hence should be included in studies of seed
and seedling survival.

Field Sites and Background to the Study

This study was conducted in Uganda, a landlocked
country in central-eastern Africa. Its area is 236,000 km^2,
of which, 42,000 km^2 is covered by water and 194,000 km^2 is
land (Hamilton 1984). Uganda is bordered by five countries:
Zaire, Kenya, Sudan, Tanzania and Rwanda, in the west, east,
north, south, and south-west, respectively (Figure 1-1).

The climate is variable, and consequently, the country is endowed with a diversity of habitats ranging from semi-deserts to tropical rain forests. Much of the country receives between 1,015 mm and 1,525 mm of precipitation in an average year (Department of Lands and Survey 1962). High precipitation coupled with favorable temperatures make Uganda an agricultural country. Crops have traditionally been classified into export (cash) and food crops (Hamilton 1984). However, under the leadership of the National Resistance Movement, some food crops (nontraditional cash crops) are also being exported.

The majority of Uganda's tropical rain forests are situated in the western part of the country (Figure 1-1) and are all under the jurisdiction of the Forest Department. Uganda, like many other tropical countries, is being deforested at a rapid rate (Van Orsdol 1983, 1986, Hamilton 1984, Struhsaker 1987, Barnes 1990, Tabor et al. 1990). It is estimated that Uganda lost 80% (24,656 km^2) of its moist forest cover between 1900 and 1980 (Barnes 1990). Although there have been some reforestation programs in the country, they have not been sufficient to reverse the downward trend.

Agriculture has by far been the most important cause of deforestation in Uganda (Hamilton 1984). The rapid spread of agriculture is closely linked with the fast growth of the human population. The food demand for increasing human population has over the years been met by increasing area under agriculture. Because forest soils lose fertility very

quickly when used for agriculture, more forest has to be cleared after a few years (Hamilton 1984).

It should, however, be noted that forest clearing is not a new phenomenon in Uganda, and that changes in forest cover in the past have not always been unidirectional (Morris and Hamilton 1974, Hamilton 1984, Hamilton et al. 1986). Using radiocarbon for dating pollen and charcoal of a peat core from Ahakagyezi swamp, south-western Uganda, Hamilton et al. (1986) asserted that the history of forest clearing stretches back to 4,800 years BP. At lower population densities, fallow periods were long enough to allow re-colonization of deforested lands (Hamilton 1984). Perhaps the first step towards reducing the rate of deforestation should begin with reducing the human population growth rate.

This study was conducted in the Kanyawara area of the Kibale Forest Reserve. The reserve lies in Kabarole District, western Uganda. The forest was first gazetted as a central forest reserve in 1948 (Struhsaker 1975). Plans to upgrade the conservation status to a forest park are underway (Forest Department 1992). The reserve covers approximately 560 km^2 (Kingston 1967, Struhsaker 1975, Forest Department 1992). It runs along a north-south axis about 56 km and is located near the edge of the western Great Rift Valley, lying only 24 km east of the Ruwenzori Mountains. The Forest is equatorial in position (0° 13' to 41' N and 30° 19' to 30° 32'E). Altitude within the reserve

ranges from 1,590 m in the north to 1,110 in the south (Struhsaker 1975).

The reserve is divided into three blocks by the Kampala-Fort Portal and Fort Portal-Kamwenge roads (Figure 1-2, Table 1-1). The three blocks are referred to as Northern, Central, and Southern Blocks (Struhsaker 1975, Forest Department 1992).

The perimeter of the reserve is about 219 km, of which approximately 148 Km is comprised of a cut-line requiring regular maintenance. The remainder follows river courses (Forest Department 1992). Areas bordered by the cut-line are vulnerable to encroachment unless the latter is maintained and patrolled regularly. Approximately 18% of the reserve was illegally transformed into farm-land in the 1970s (Van Orsdol 1983, 1986, Hamilton 1984, Forest Department 1992). In 1992, however, government succeeded in evicting encroachers from the reserve. Plans to restore the former encroachment areas are in progress (Isaac Kapalaga, Pers. Comm.).

Many areas in the north and central blocks were logged between 1950 and 1968 (Struhsaker 1975, Kasenene 1987, Skorupa 1988). The logging program has now been suspended, and the Forest Department is formulating alternative ways of developing this resource for socioeconomic purposes that are compatible with the long-term objectives of maintaining Kibale's natural diversity and environmental benefits.

In the new management plan (Forest Department 1992), the forest has been divided into zones for management purposes. Some of these are new, while others are modifications of the already existing zones (Figure 1-3). Kanyanchu area was designated a recreation zone, and a tourist facility was set up in this area. This represents a new development in the management of Kibale Forest. Tourism at Kanyanchu has already started and its future is promising provided the political environment does not deteriorate.

Realizing the importance of research in formulating sound management policies, the area for research was expanded. In addition to research plot 703 which existed in former management plan, all areas where Makerere University Field Biological Station (MUBFS) has conducted long-term research were also added to the research zone (Figure 1-3). These include compartments K13, K15, K28, and K29.

A narrow strip of forest along the eastern and north-western borders were designated community use zone. Natural resources can be collected by local people in this zone. However, the details of resource use have not been worked out (Isaac Kapalaga Pers. Comm.).

The Climate

The climate in the reserve could be generalized as rainy and warm (Struhsaker 1975, Kasenene 1987). Although rainfall is heavy, and fairly well distributed throughout the year, the reserve experiences dry and wet seasons.

March-April and September-November are wetter than the other months. June-July and December-February are usually drier months. The June-July dry season is more severe than the latter (Kingston 1967).

The mean annual rainfall measured at Fort Portal (nearest meteorological station) for 52 years prior to 1967 was about 1474.5 mm (Kingston 1967). Within the reserve, the total rainfall varies along its length from north to south. A maximum rainfall of 1473.2 mm was recorded near Sebitoli in the north, this decreased to 1393 mm in the south (Kingston 1967). Temperatures are moderate and do not fluctuate much over the year. The mean minimum and mean maximum for Fort Portal are 12.7 ^{o}C and 25.5 ^{o}C, respectively (Kingston 1967).

The Vegetation

Kibale Forest is a mosaic of vegetation types and is consequently difficult to describe in simple terms (Struhsaker 1975). Only 60 % of the reserve is dominated by trees; the remaining 40 % is composed of grasslands, woodlands, thickets, colonizing forest, papyrus swamps, and plantations of exotic trees (Wing and Buss 1970). Grasslands are dominated by *Pennisetum purpureum* Schum., *Imperata cylindrica* Beav, and *Cymbopogon afronardus* Schult. (Kasenene 1987). In the forested area, tree canopies usually lie between 10 m to 30 m with some trees over 55 m in height (Struhsaker 1975, Rudran 1978, Butynski 1990).

Grasslands, thickets, and colonizing forests occur on higher hills formally occupied by Batooro tribesmen prior to the sleeping sickness epidemic which swept across western Uganda early this century (Osmaston 1959, Wing and Buss 1970). The northern sector of the forest has been classified as *Parinari* forest, because the upper canopy is dominated by this large conspicuous emergent tree. Co-dominants in this area include *Carapa*, *Aningeria*, *Newtonia*, and *Olea wilwitschii*. As one moves to the south, *Pterygota*, *Piptadeniastrum* and *Chrysophyllum albidum* become obvious elements in the forest (Kingston 1967). Close to the southern end of the reserve, the forest is dominated by *Cynometra alexandri*.

The Mammalian and Avian Fauna of Kibale Forest

Habitat diversity within the reserve, coupled with its geographical location at the interface of East and Central Africa, results in a diverse mammalian and avian fauna (Struhsaker 1975). Another factor contributing to the high diversity of avian and mammalian fauna of Kibale is its proximity to the Pleistocene refugia (Struhsaker 1981). Distance from the forest reserve to the refugia was positively correlated with number of anthropoid primate species in the reserve (Struhsaker 1981). This relationship probably extends to the other animal species. As many as 304 species of birds belonging to 52 families have been recorded from Kibale and its surroundings (Skorupa 1983).

Common large mammals living in the Kibale Forest
Reserve include bush buck (*Traglephus scriptus*), Harvey's
red duiker (*Cephalophus natalensis*), giant forest hog
(*Hylochoerus meinertzhageni*), and the bush pig
(*Potonmochoeus porcus*). The elephant (*Loxodonta africana*)
population was greatly reduced in the 1970s, but current
research (Edgar Buhanga Pers. Comm.) indicates that the
population is increasing. Less common are buffalo (*Syncerus
cafer*), ratel (*Mellivora capensis*), crested porcupine
(*Hystrix* sp), and Serval cat (*Felis serval*). Lions
(*Panthera leo*) occasionally visit the study area. Leopards
(*Panthera pardus*) are suspected to be coming back to the
study area (Jessica McCoy, David Watts Pers. Comm.).
Hippopotamus (*Hippopotamus amphibius*) are present in the
southern end of the reserve, but do not occur in the study
area.

The forest contains a high diversity of small mammals.
Sixteen species of rodents have been caught in the Kanyawara
area (Muganga 1989). Also present are shrews (*Crocidura*
spp) (Muganga 1989, Anke Hoffmann Unpublished). Several
species of squirrels, including the flying squirrel
(*Anomalurus* sp) (Struhsaker 1975), inhabit the forest
canopy.

Kibale Forest has a rich primate fauna. This includes
the red colobus (*Colobus badius tephrosceles*), Black and
white colobus (*Colobus guereza*), blue monkeys (*Cercopithecus
mitis stuhlmanni*), redtail monkeys (*Cercopithecus

ascanius), l'Hoesti's monkeys (*Cercopithecus lhoesti*), grey cheeked mangabeys (*Cercocebus albigena johnstoni*), baboon (*Papio anubis*), chimpanzee (*Pan trogldytes*), Potto (*Perodictus potto*) and two species of galagos (*Galago demidovii*) and *Galago inustus*).

History of the Study Plots

Compartment K30

The study plot was approximately 300 ha of relatively undisturbed forest, representing typical *Parinari* forest type (Struhsaker 1975, Kasenene 1987, Skorupa 1988). Prior to 1970, a few large trees (3-4 commercial trees/ Km^2) were removed by pitsawyers (Struhsaker 1975). This felling intensity was below the natural rates of treefall in K30 (approximately 370 trees / Km^2 /year; Skorupa & Kasenene 1984), and probably did not alter the integrity of the forest appreciably. This compartment was used in previous rodent studies (Isabirye-Basuta 1979, Kasenene 1984, Muganga 1979). K30 was used as the control in this study because of its relatively undisturbed nature and the existing baseline data on rodent populations.

Compartment K15

This includes approximately 360 ha of mechanically selectively felled forest (Skorupa 1988). Felling occurred between September 1968 and April 1969 (Kasenene 1987, Skorupa 1988). Although only approximately 7.4 - 8.6

commercial trees, or 21 m^3 were removed per hectare (Kasenene 1987, Skorupa 1988), the forest canopy was opened by 62% (Kasenene 1987). Rodent populations in this forest were previously studied by Muganga (1989).

Compartment K13

This compartment included 622 ha of forest. It was mechanically selectively logged between April and August 1968 (Skorupa 1988). Approximately 17 m^3 or 6.1 - 9.8 commercial trees were removed per hectare (Kasenene 1987, Skorupa 1988). In addition to logging, non-commercial tree species were treated with arboricides (Kasenene 1987, Skorupa 1988).

Table 1: Areas of the three blocks comprising Kibale Forest
Reserve.

Block	Area (ha)
Northern Block	1,354
Central Block	36,296
Southern block	18,592
Total	56,242

Source: Forest Department (1992).
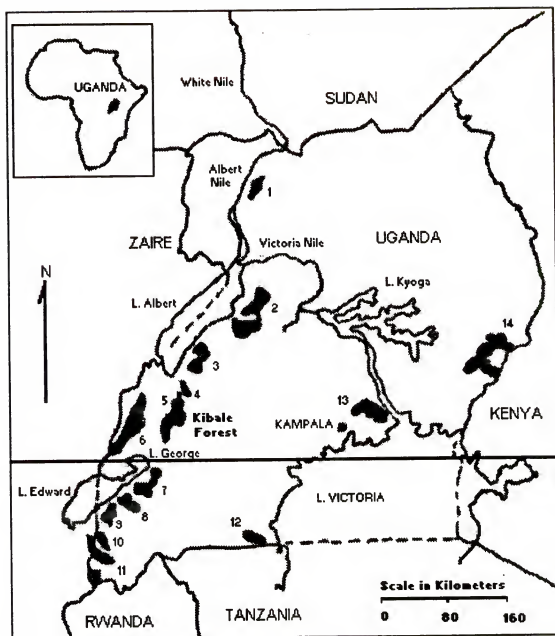
Figure 1-1: Map of Uganda showing major forest reserves and some geographical features. Forest reserves include: 1-Zoka, 2-Budongo, 3-Bugoma, 4-Itwara, 5-Kibale, 6-Rwenzori, 7-Kashoya-Kitomi, 8-Kalinzu, 9-Maramagambo, 10-Impenetrable (Bwindi), 11-Mgahinga, 12-Malabigambo, 13-Mabira, and 14-Mount Elogon.
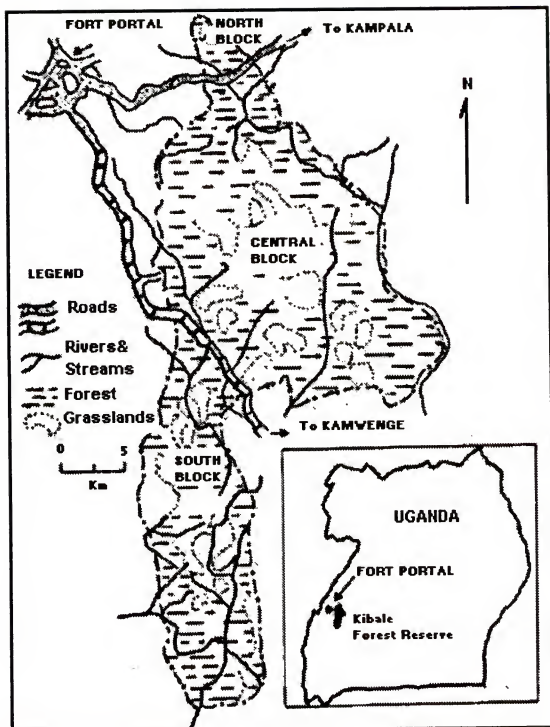
Figure 1-2: Map of the Kibale Forest Reserve showing the major roads, rivers, streams and the three administrative blocks of the reserve. Research was conducted in the central block.
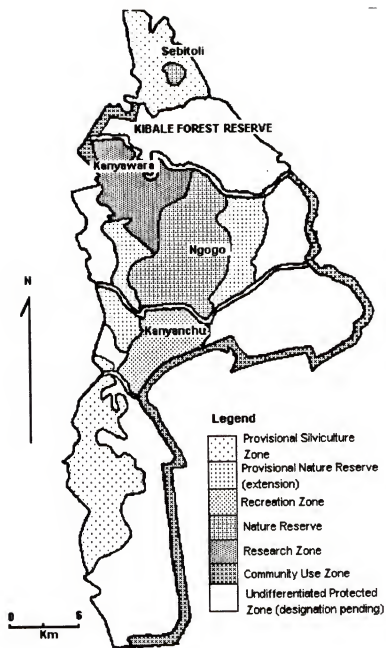
Figure 1-3: Map of the Kibale Forest Reserve showing
management zones stipulated in the 1992 management plan.
This work was conducted in the Kanyawara area, designated
for research.

CHAPTER 2

SEED PREDATION IN MATURE AND SELECTIVELY LOGGED FOREST
COMPARTMENTS

Introduction

The importance of forest gaps in the regeneration of
tropical forest has been recognized for at least three
decades (e.g., Schulz 1960, Bazzaz and Pickett 1980,
Hartshorn 1978, Denslow 1980, 1987, Kasenene 1987, Denslow
et al. 1990). As Schupp and Frost (1989) noted, the
majority of these studies (e.g., Gelmond 1978, Ng 1978,
Whitmore 1978, Augspurger 1979, Bazzaz and Pickett 1980,
Garwood 1983, Brokaw 1985 Denslow 1980, 1987, Fetcher et al
1985, Foster & Janson 1985, Sork 1985, Denslow et al. 1990,
Brown 1993) focused on physiological and growth responses of
plants to the altered environment in gaps. They showed that
seedlings of small-seeded species grow faster in response to
light than those of large-seeded species. Hence, saplings
and poles of large seeded tree species were less likely to
dominate canopy gaps unless they were present prior to gap
formation.

In addition to competitive exclusion by pioneer
species, rarity of juveniles of large-seeded species in gaps
may also be influenced by animals that consume large seeds
and their seedlings. Unfortunately, the importance of
animals in gap dynamics has received attention from only a

few ecologists (e.g., Hartshorn 1978, Schupp 1988a, Webb & Wilson 1985, Schupp and Frost 1989, Turner 1990). Another possible explanation of rarity of juveniles of large-seeded species in gaps is that seeds never arrive, or if they do, they are at low densities (see Denslow & Diaz 1990). Large seeds in tropical forests are dispersed mainly by arboreal mammals such as monkeys and by birds whose movements, and hence seed dispersal, may be affected by gaps. For example, lack of perching sites for birds, and lack of continuous arboreal 'paths' in the case of primates may prevent these animals from using an area.

Seed predation is another possible explanation of rarity of large seeded species in forest gaps. Hartshorn (1978) was possibly the first to address the importance of seed predation in gap dynamics. He based his predictions on the escape hypothesis (Howe and Smallwood 1982), which was proposed independently by Janzen (1970) and Connell (1971). It predicts that seeds and seedlings beneath parent plants would suffer disproportionately higher mortality than those further away from the parents. Hartshorn (1978) predicted that seed survival would be higher in gaps than in the understory, because seeds in gaps are likely to be at low density and distant from adult trees of the same species. Nonetheless, data from studies comparing seed/seedling predation in gaps and in understory have been inconsistent. Webb & Willson (1985) and Turner (1990) reported greater seedling survival in gaps for some species, but other

studies found that seed survival in gaps was less than (Schupp 1988 a) or equal to (Webb and Willson 1985) survival in the understory. The advantage of distance from parent and low density conferred by gaps may be counteracted by high density of seed/seedling predators and competition in gaps.

If seed survival is solely determined by seed density and distance from parents, as predicted by the escape hypothesis, one would expect highest survival in large gaps such as those created by logging. However, logged forests usually fail to regenerate from seeds due to a combination of factors including seed predation (Kasenene 1984, Isabirye-Basuta & Kasenene 1987). Logging creates extensive gaps that become dominated by herbaceous tangles or thickets that form a more or less continuous cover (Kasenene, 1987, Okali & Ola- Adams 1987). Several studies (e.g., Janzen 1970, 1971, Delany 1971, Synnott 1975, Kasenene 1984, Isabirye-Basuta & Kasenene 1987, Muganga 1989, Walker & Rabinowitz 1992) have shown that thick ground cover favors small mammal populations. Some studies (e.g., Sork 1987, Schupp et al 1989,) have concluded that seed predation by small mammals such as rodents is the most important cause of seed and seedling mortality in forest gaps. Large seeds are particularly prone to post-dispersal predation by small mammals (Janzen 1969, 1971, Harper 1977, Howe & Richter 1982, Denslow 1987). Therefore, the formation of large gaps

not only lowers chances of seed dispersal, but also attracts small mammals that eat large seeds.

Most experimental studies on post-dispersal seed predation (e.g., Perry and Fleming 1980, Mittelblach and Gross 1984, Kasenene 1987, Tsingalia 1988, Willson and Whelan 1990) have investigated the influence of size of the seed piles on seed survival. In nature, large seeds are often dispersed singly. Results are presented here from experiments designed to mimic natural dispersal and compare survival of sparsely dispersed seeds of two canopy forest species *Mimusops bagshawei* (S. Moore) and *Strombosia schleffleri* (Engl.), in gaps and understory of a mature and a logged forest.

Objectives and Hypotheses

The main objective of this study was to examine the influence of logging and gaps on post dispersal seed predation. Specially, I hypothesized that

(i) seed predation was higher in the logged forest than in the mature forest, because in previous studies in Kibale rodents (seed predators) were more abundant in the former than in the latter (Isabirye-Basuta 1979, Kasenene 1984, Isabirye-Basuta & Kasenene 1987, Muganga 1989).

(ii) seed survival was higher in the understory than in gaps because rodents forage more frequently in gaps than in the understory (Schupp & Frost 1989).

I also attempted to: (i) examine differences in seed survival between understory and gaps of a mature and logged forest.

(ii) to determined the influence of small and large mammals on the survival of sparsely dispersed seeds and

(iii) the habitat characteristics that influence seed survival.

Methods and Materials

Study Species

Strombosia scheffleri (Olacaceae) is a common canopy species in the northern and central blocks of Kibale Forest Reserve (Struhsaker 1975). Skorupa (1988) found that densities of trees (dbh $\geq$ 10 cm) were 20.6 stems/ha and 2.9 stems/ha in the mature and selectively logged forests, respectively. Nonetheless the low density of *Strombosia* trees in the logged forest is not due entirely to logging. According to Forestry Department records, no *Strombosia* stems were removed by the loggers although the species was commercially important at that time (Skorupa 1988).

The mature fruit of *Strombosia* is approximately 20-25 mm in diameter (Eggeling & Dale 1951). Unripe fruits (Struhsaker 1978a) and seeds (Struhsaker 1975) are eaten by red colobus monkeys (*Colobus badius tephlosceles*). Fruits are eaten by blue monkeys (*Cercopithecus mitis Stuhlmanni*), redtail monkeys (*Cercopithecus ascanius*), mangabeys

Cercocebus albigena (Struhsaker pers. comm). Seeds are dispersed over long distances by bats (Personal observation). Mean weight of fresh seeds collected at Kanyawara in 1992 was (mean = 3.25 g, S.D. = 0.82 g, N = 165).

Mimusops bagshawei (Sapotaceae) is another canopy species in Kibale Forest. Its density (dbh $\geq$ 10 cm) was estimated at 2.3 stems/ha in the mature forest and, 0.5 tree/ha in the logged forest (Skorupa 1988). Intense searching in the logged forest located 14 adult trees in the 1 Km^2 study area. A negligible volume (< 0.01 m^3/ha) of *Mimusops* was extracted by the loggers from this forest in the 1960s (Skorupa 1988). Hence, the low density of *Mimusops* in this forest(K15), cannot be explained by logging alone.

Ripe fruits of *Mimusops* are 25 mm long (Eggeling & Dale 1951). They are fed upon and dispersed by mangabeys (*Cercocebus albigena*) (Waser 1974), redtails (Struhsaker 1978 b Lwanga 1987), blue monkeys (Lwanga 1987), chimpanzees (Ghilglieri 1984), and several frugivorous birds. Immature and ripe fruit and seeds are consumed by red colobus monkeys (Struhsaker 1975, 1978 a).

Experimental Design

The effects of logging, gaps, and the exclusion of rodents and large mammals on seed disappearance and germination were tested in the mature forest (K30) and

logged forest (K15). In the mature forest, 30 gaps of varying sizes were selected along existing trails (mean gap size = 182 m^2, range = 33 m^2 to 823 m^2). Understory sites for experimental treatments were located 20 m from the edge of each gap. Compartment K15 was severely damaged during the logging operations, and the entire study area was predominantly gap in nature. Average gap size was 1307 m^2, range = 73 m^2 to 7100 m^2 (Kasenene 1987). For this reason, 30 forest patches (Average patch size = 586 m^2, range = 125 m^2 to 2709 m^2) instead of gaps were selected. Gap sites for experimental studies were located 20 m from the edge of each forest patch. In both forests, the experiment was restricted to mid and upper slopes. Valley bottoms were avoided, because in both logged and unlogged areas they are usually open and the ground is covered with thick and distinctive vegetation, different from the other forest habitats.

In each gap in the mature forest, and in each forest patch in the logged forest, five seed stations were established. All stations were placed in the center of the gap or forest patch. Distance between stations was to an extent dictated by size of the gap or forest patch, but was always at least 2 m. Six seeds were placed at each station: For both *Mimusops* and *Strombosia*, one seed of each species was placed on the forest floor with no predator exclosure (control); One seed of each species was placed on the ground and was enclosed in a cage that excluded large

mammals (duikers), but allowed in small mammals (rodents); Another seed of each species was enclosed in the same mesh wire cage that excluded both large and small mammals. The cost of mesh wire prohibited using separate cages for each seed species. Treatments were replicated in the mature forest understory, 20 m from each gap, and in the 'gap' environment of the logged forest, 20 m from each forest patch.

Large mammal exclosures (Figure 2-1) were conical in shape, 1 m tall, and 50 cm in diameter and constructed from mature stems of elephant grass (*Pennisetum purpureum* Schum) fixed into the ground at 10 cm intervals. Stems converged at the top and were tied together with banana fibers. Spaces of 10 cm between elephant grass stems were large enough to permit the entry of rodents, but medium to large mammals could not gain access to the seeds.

Rodent exclosures were constructed from 2 mm X 2 mm wire mesh. These were conical structures of approximately 30 cm in height and about 20 cm in diameter. They were held firmly on the ground by two wooden pegs that formed an inverted V over the cage. Seeds were pressed a few millimeters into the soil (but not buried) to reduce chances of being washed away by rain. Care was taken not to place seeds under fruiting trees of the same species.

All fruit was removed from the seeds of *Strombosia* and *Mimusops* to ensure that animals were not attracted by the fruit but by actual seeds. Therefore, it was assumed that

all seeds that disappeared in this study were eaten by seed predators.

The Monitoring Schedule

The experiment was conducted in two study phases. In the first phase, control seeds of *Strombosia* were placed at seed stations on July 1 and 2 1992 in the mature and logged forests, respectively. *Strombosia* seeds were placed in exclosures in both forests one month later, and seeds of *Mimusops* were placed into all treatments at that time. This study was terminated on October 26, 1992, when over 75% of the control seeds had been eaten. Control seeds of *Strombosia* had been monitored for 115 days during this study phase; all other seeds had been monitored for 87 days.

During the second phase of the experiment, the studies were repeated and seeds in all treatments were monitored for up to 241 days. The second phase began on October 28 1992, in the mature forest, and on October 29 1992, in the logged forest. Routine observations were terminated on February 2 1993, in the mature forest, and on February 3 1993, in logged forest. However, seeds that had not been eaten were left in place and censused again on June 26 and June 27 1993, in the mature forest and the logged forest, respectively.

Seed stations were checked every other day for the first 18 days. Thereafter, they were visited weekly. In the first phase, experimental seeds that became covered by

falling leaves were uncovered during the census. This probably accelerated the rate of seed predation. In the second phase, leaf litter was restored after observations on the seed were made.

During each visit, the following were noted:

1) Presence or absence of seeds

2) Damage; fungal infection and rot.

3) Evidence of germination.

4) Presence or absence of any remnants, e. g, seed coat and/or seed debris.

Estimation of Environmental Variables at Seed Stations

At every seed station, ground vegetation cover (GVC), canopy openness, litter depth, volume of wood (fallen stems and branches $\geq$ 10 cm dbh), gap size (in mature forest), and forest patch size (in logged forest) were estimated. To make these measurements, the longest axis in a gap or a forest patch for mature and logged forests, respectively, was divided into 5-m intervals. Gap edge was determined based on the cut-off point of gap vegetation dominated by creepers and large leafed herbaceous plants (Kasenene 1987). At 5-m intervals, I estimated ground vegetation cover in 1 m^2 quadrats that were subdivided into four equal sub-plots using two strings. Percent ground vegetation cover of plants under 1.3 m was estimated visually for each sub-plot, and the average was recorded. At the center of the quadrat, litter depth was estimated by hammering a 2-cm-diameter PVC

tube into the ground. The tube was slit so that the contents could be read against a ruler. Litter depth was equal to length of all contents minus length covered by soil.

Canopy openness was estimated by looking at the canopy through a tube (diameter = 8 cm) which was covered with a transparent plastic sheet on which 16 one-cm^2 squares were marked. The number of squares through which the sky could be seen was recorded as canopy openness.

The above exercise was repeated at 5-m intervals. The number of samples in each gap or forest patch depended on length of the longest axis. The mean of each variable was recorded for that location. Volume of wood in the gap, in mature forest, or in the forest patch, in logged forest, was estimated by measuring length and diameters of all logs greater or equal to 10 cm. Volume was calculated using the following formula: Volume = $3.14(r^2h)$; where r is the radius and h is the length of fallen stem or branch. It was assumed that all fallen wood was cylindrical.

Beginning at the interface, the same procedure was subsequently continued 20 m into the understory in the mature forest, and 20 m in the 'gap', in the logged forest. The exercise was repeated along equal distances as the longest axis of the corresponding gap or patch. Direction followed that of the corresponding gap or forest patch.

Gap and patch size were estimated by measuring out perpendicular distances from the longest axis to the edge.

These distances were taken at 5 m intervals and were drawn
to scale on graph paper and areas were calculated.

Statistical Analysis

The one-way ANOVA was employed to test for differences
in habitat variables and duration of seed survival among the
four habitat types, i.e., gaps and understory of the mature
forest and gaps and understory of the logged forest. Once
differences were detected with the ANOVA, the Scheffe's
procedure ($p < 0.05$) was used to identify averages that were
different from one another for all possible pair
combinations. The t-test was employed to test for
differences between number of days survived by control seeds
in the mature and logged forests. In this analysis, gap and
understory samples for each forest were combined; thus,
sample size was 60 in each forest.

Differences in seed survival among control, large
mammal exclosures, and rodent exclosures were tested
employing the one-way ANOVA. Differences between any pair
of treatments were tested with the Scheffe's procedure ($p < 0.05$).

The logistic regression, which is the equivalent of the
multiple regression for continuous variables, was developed
to examine the functional relationship between a binomial
dependent variable and an independent variable that may
either be discrete or continuous (Trexler and Travis 1993).

This analysis was employed to examine the influence of ground vegetation cover, litter depth, volume of wood, and canopy openness on the probability of survival of *Mimusops* and *Strombosia* seeds in a logged and a mature forest compartments. Presence or absence of seeds were the dependent variables. The analyses were performed when routine censusing was terminated at day 87 and day 95 for study phase 1 and study phase 2 seeds, respectively.

The 2 X 2 contingency G-test (Sokal & Rohlf 1969) was employed to test for proportions of phase 2 *Mimusops* and *Strombosia* seeds that germinated in gaps and understory of the two forests when rodents were excluded. Two questions were addressed:

1) If rodents (major seed predators) are excluded, does seedling establishment differ among gaps and understories of mature and logged forest? And 2) Under natural conditions (control) does seedling establishment differ among the four habitat types mentioned above?

Seeds that disappeared or were damaged prior to termination of routine censusing were recorded as eaten. Seeds that were recovered after 241 days were recorded as rotten if they disintegrated under the force between my forefinger and thumb. Three seeds that had not rotted were recovered in rodent exclosures in gaps of the logged forest. These were recorded as live seeds but may not have been viable. Seeds that were eaten by rodents from rodent

exclosures, and those classified as unknown (Tables 2-6 and
2-7), were excluded from the analysis.

Results

Habitat Analysis

Habitat variables, canopy openness, ground vegetation
cover, litter depth, and volume of fallen wood varied
considerably within and among habitat types (Table A.1).
Canopy openness differed among the four habitat types (Table
2-1). Canopy openness of the mature forest was the lowest
but did not differ from that of forest patches in the logged
forest. Gaps of the logged forest were significantly more
open than those in the mature forest (Table 2-1).

Ground vegetation cover trends were similar to those
for canopy openness, and were significantly different among
the four habitat types (Table 2-1). Ground vegetation cover
was lowest in the understory of the logged forest followed
by the understory of the mature forest but the two were not
statistically different. Ground vegetation cover was higher
in gaps of the logged forest than in gaps of the mature
forest (Table 2-1).

Litter depth was different among the four habitat types
(Table 2-1). It was lowest in gaps of the logged forest,
followed by gaps of the mature forest and by the understory
of the mature forest. Average litter depths of these three
habitats were not significantly different, but all were

significantly lower than litter depth in the understory of the logged forest.

The rank order in volume of wood from lowest to highest was as follows: gaps of the logged forest, understory of the mature forest, understory of the logged forest and gaps of the mature forest. However, differences among the first three were not significant, and all were significantly lower than the volume of wood in the gaps of the mature forest (Table 2-1).

Influence of Large and Small Mammals on Survival of Sparsely Dispersed Seeds

Date of seed predation was estimated as the mid-point between the day when the seed was previously observed and the day when it was first recorded absent or damaged by a predator. The longest interval between observations was a week. Sometimes rodents (judging from tooth-marks) made small bites on *Strombosia* seeds and left them on the spot. These seeds were considered dead or preyed upon when the bites were observed because these seeds usually disappeared within a few days or were infected and killed by fungi. Few *Strombosia* seeds that were killed by fungi after the initial bite were later consumed by rodents. Seed survival was higher and less variable in rodent exclosures than in large mammal exclosures and control (Tables A.2 and A.3).

Mimusops seeds were sometimes eaten on the spot, as evidenced by the remaining seed coat, suggesting that the

predator was a rodent. In most cases, however, the whole
seed disappeared; hence the predator could not be
determined.

No predation was expected in the rodent exclosures, but
in a few cases, rodents dug underneath the cages and ate the
seeds. This observation however, substantiates the
assertion that seeds that disappeared in the control and
large mammal exclosures were eaten by rodents.

For both *Mimusops* and *Strombosia*, there were highly
significant differences in average number of days survived
by seeds among treatments in both phase 1 and phase 2
(Tables 2-2 and 2-3). The average survival of *Mimusops* and
Strombosia seeds did not differ between control and large
mammal exclosures in phase 1 and phase 2 in three of the
habitat types: gaps of mature forest, understory of mature
forest, and gaps of the logged forest (Tables 2-2 and 2-3).
With the exception of the understory of forest patches in
the logged forest during study phase 2, seeds of both
Mimusops and *Strombosia* that were in rodent exclosures
survived significantly longer than those in control and
large mammal exclosures (Tables 2-2 and 2-3). In the
second phase, there was a general increase in seed survival
regardless of exclosures in the understory of the logged
forest, possibly due to accumulation of litter over the
seeds. During the second study phase, seeds of *Mimusops*
that were in rodent exclosures in the understory of the
logged forest did not survive significantly longer than

those in large mammal exclosures (Table 2-2). During the same phase, *Strombosia* seeds that were in rodent exclosures in the understory of the logged forest did not survive longer than those that were in the open (control seeds) (Table 2-3). During the second study phase, *Strombosia* control seeds in the understory of the logged forest survived longer than those in large mammal exclosures. This observation suggests that large mammal exclosures possibly attracted seed predators. Because no damage was observed on exclosures with missing seeds, it is most likely that seeds were removed by small mammals.

Survival of *Mimusops* and *Strombosia* Seeds in Gaps and Understory of Mature and Logged Forest Compartments

Two predictions were tested: 1) average seed survival should be higher in the understory than in gaps, and 2) seed survival should be higher in the mature forest than in the logged forest. In this analysis, only seeds under control conditions were considered.

Data from the first study phase (leaf litter was removed from seeds) indicated no significant difference in survival of *Mimusops* seeds among the four habitat types (Table 2-4). However, in the second phase (leaf litter not removed from seeds), a significant difference in mean number of days survived by *Mimusops* seeds among the four habitat types was detected. The significant difference was between average survival in the understory and gap of the logged

forest only. As predicted, average survival was higher in the understory than in gaps (Table 2-4), suggesting that seed predators were more abundant in gaps, or foraged more frequently in gaps than in the understory. Comparisons of survival of *Mimusops* seeds between mature and logged forest did not yield significant differences (t = 0.014, p > 0.1, df = 118) and (t = 0.17, p > 0.1, df = 118 for study phases one and two, respectively).

For *Strombosia*, a significant difference in average number of days survived by seeds among the four habitat types was detected in the first study phase (Table 2-4). The only significant difference was between average seed survival in the understory of the logged forest and in gaps of the mature forest (Table 2-4). The difference in average seed survival between understory and gaps of the logged forest was not significant. However, a paired t-test (which controlled for extraneous variation due to locations) between these two habitat types revealed a significant difference in seed survival (t = 3.02, p < 0.005). As predicted, average seed survival was higher in the understory than in gaps (Table 2-4). Contrary to expectation, *Strombosia* seeds survived longer in the logged forest than in the mature forest in the first study phase (t = 2.70, p = 0.0078, df = 118).

In the second study phase, there was a highly significant difference in the average survival of *Strombosia* seeds among the four habitat types (Table 2-4). Seed

survival in the understory of the logged forest was significantly higher than seed survival in the other habitat types. There were no differences in seed survival among gaps and understory of the mature forest and gaps of the logged forest (Table 2-4). Nonetheless, a paired t-test for differences between average seed survival in the understory and in gaps of the mature forest indicated that average seed survival was higher in the understory than in gaps (t = 2.82, p = 0.009 df = 28). In the second study phase, contrary to expectation, *Strombosia* seeds survived longer in the logged forest than in the mature forest (t = 3.08, p = 0.0026, df = 118).

Habitat Correlates of Seed Survival in Logged and Unlogged Forest Compartments

During the first study phase, the logistic regression showed no significant relationships among ground vegetation cover, litter depth, volume of wood, and canopy openness, and the probability of seeds being present at day 87 for all control seeds (when seeds were kept free of litter) in either forest compartment. Similarly, there was no relationship between any of the mentioned habitat characteristics and the probability of seed presence at day 95 for all control seeds in the mature forest in the second phase.

When number of days survived by *Mimusops* and *Strombosia* seeds during phase one was correlated with ground vegetation

cover, volume of wood and litter depth, results agreed with those of the logistic regression, yielding no significant correlations, with one exception. A positive correlation between survival of *Strombosia* phase one seeds and litter depth ($r = +0.3029$, $p < 0.01$, df 58) was detected in the logged forest, suggesting that large amounts of litter on the ground may increase seed survival. Correlations of number of days *Mimusops* and *Strombosia* seeds survived during phase two with ground vegetation cover, litter depth and volume of wood were not significant, as indicated by the logistic regression; except in the mature forest where survival of *Strombosia* seeds was negatively correlated with ground vegetation cover ($r = -0.303$, $p < 0.01$, df = 58).

In the logged forest, a stepwise logistic regression revealed that the probability of *Mimusops* and *Strombosia* seeds being present at day 95 (second study phase seeds) was negatively related to ground vegetation cover for both (Table 2-5). In the stepwise logistic regressions, canopy openness did not contribute significantly to the fitness of the model for both seed species. However, when regressed separately, (simple logistic regression) canopy openness was significantly negatively related to the probabilities of both seed species being present at day 95 (Table 2-5). The probability of a *Strombosia* seed being present at day 95 was significantly and positively related to litter depth in the logged forest compartment (Table 2-5)

The Fate of *Mimusops* and *Strombosia* Seeds After 241 Days

The number of *Mimusops* seeds that became established seedlings in rodent exclosures ranged from 4 in the understory of the mature forest to 13 in both the gaps and understory of the logged forest (Table 2-6). In the mature forest significantly more seedlings established themselves in gaps than in the understory (G = 4.9, p < 0.05, df =1). The majority of seeds in the understory rotted (Table 2-6). In the logged forest, 13 *Mimusops* seedlings became established in both gaps and understory. More seeds in understory rodent exclosures were either eaten by rodents, or classified as unknown than in gap rodent exclosures (Table 2-6). These were excluded from the analysis. Nonetheless, the difference in number of established seedlings between gaps and the understory was not significant (G = 0.51, P > 0.1, df = 1). When gap and understory rodent exclosures were combined in each forest, more *Mimusops* seeds became established seedlings in the logged forest than in the mature forest (G = 5.23, p < 0.05, df = 1). These results suggest that, establishment of *Mimusops* seedlings would be higher in the logged forest than in the mature forest if rodents were excluded. Rotting was a major cause of mortality for *Mimusops* seeds in rodent exclosures particularly in the understory (Table 2-6). More *Mimusops* seeds in rodent exclosures succumbed to fungal infection in the mature forest than in the logged forest (G = 4.40, p < 0.02, df = 1).

For *Strombosia*, the number of seeds that became established seedlings in rodent exclosures varied between 12 and 15 (Table 2-7). There were no significant differences in seedling establishment between gaps and understory of the mature forest (G = 0.006, p > 0.1, df = 1), and between gaps and understory of the logged forest (G = 0.0006 p > 0.1, df = 1), when rodents were excluded. There was no difference between number of *Strombosia* seeds that became established seedlings in the mature and logged forests when rodents were excluded (G = 0.0004, p > 0.1, df = 1).

None of the *Mimusops* control seeds in the understory of mature forest, gaps of the mature forest, or in gaps of the logged forest became established seedlings. Three seedlings became established in the understory of the logged forest.

None of the *Strombosia* control seeds became established seedlings in gaps and understory of the mature forest compartment. All were eaten by predators before 95 days (Table 2-7). In the logged forest, however, one seedling established in a gap and five seedlings established in the understory.

Discussion

Some of the habitat variables considered in this study, such as ground vegetation cover and litter depth may be important in the ecology of seed predators. Hence, they may influence the survival of seed and seedlings, which in turn will affect forest regeneration. For example, ground

vegetation cover was found to correlate negatively with seed survival, at least in the logged forest. Working in the same forest, Kasenene (1984) also found a negative correlation between seed survival and ground vegetation cover, further supporting the assertion that thick ground cover has a negative influence on the survival of large seeds. In the second phase of my experiment, when leaf litter was allowed to accumulate on the experimental seeds, average seed survival was significantly greater in the understory for both *Mimusops* and *Strombosia* seeds in the logged forest. The patches of forest in the logged forest had the highest amount litter on the ground, and the lowest ground vegetation cover compared to the rest of habitat types. In addition, average seed survival of control seeds was fairly high in the forest patches. These observations suggest that forest patches offer more suitable conditions for seed survival than elsewhere.

When litter was allowed to accumulate over experimental seeds, there was a positive relationship between litter depth and the probability of *Strombosia* seeds being present after 95 days in the logged forest. This observation strengthens the suggestion that litter may play an important role in seed survival. The observation is consistent with the findings of Estrada and Coates-Estrada (1991) at Los Tuxtlas, who found a drastic decrease in rodents' ability to detect seeds that were buried below 2.5 cm. Higher seed and seedling survival in the understory than in gaps was

attributed to lower frequency of rodent foraging in the former than in the latter (Schupp 1988a Schupp & Frost 1989). This study shows that differences in litter depth between gaps and understory may also influence seed survival.

Most comparisons (except for *Strombosia* in second season) between gaps and understory of the mature forest were not significant, probably because gaps in the mature forest are smaller than the average home range of the Kibale rodents (range of averages = 500 m^2 - 1400 m^2, Isabirye-Basuta 1979). Each gap probably included home ranges of several rodents. Additionally, the rodent population was unusually high during this study (Chapter 4) and possibly masked the normal seed predation patterns.

Identity of Seed Predators

From exclusion experiments, it appears small mammals such as rodents were the most important cause of seed mortality. Exclusion of rodents increased seed survival in all four habitat types. The conclusion that rodents are the most important seed predators in the wild is supported by several field studies (Schupp 1988 a & b, Whelan et al. 1990, Estrada and Coates-Estrada 1991).

The hypothesis that seed survival should be higher in the mature forest and particularly more so in the understory of the mature forest than in the logged forest was not supported by the data. This hypothesis was based on results

from previous studies in Kibale (e.g., Isabirye-Basuta 1979, Kasenene 1984, Isabirye-Basuta & Kasenene 1987, Muganga 1989) in which more rodents were caught in logged forest compartments than in the mature forest compartment.

In 1992, there was an abundant crop of *Strombosia* seeds in the mature forest (May through September 1992); this was followed by another huge crop of *Mimusops* seeds starting in November 1992. In the logged forest, there were no *Strombosia* seeds. Furthermore, the *Mimusops* crop in the logged forest was smaller than in the mature forest, because *Mimusops* trees occurred at low density in the logged forest, and few trees fruited there. Most likely, rodents in the mature forest responded numerically to the abundant seed supply. Consequently, their populations were higher in the mature forest than in the logged forest during this study (Chapter 4) and exerted greater predation pressure on the experimental seeds. Thus, my study was exceptional and contrary to previous rodent studies in Kibale (e.g., Isabirye-Basuta 1979, Kasenene 1984, Isabirye-Basuta & Kasenene 1987, Muganga 1989).

The Importance of Seed Predation on Gap Dynamics

The majority of scientific work published on gap dynamics (Whitmore 1978 Bazzaz and Pickett 1980, Saulei 1984, Brokaw 1985, Denslow 1987, Denslow et al. 1990) has emphasized the importance of physiological aspects in plants' ability to occupy gaps. Seeds of pioneers (small-

seeded trees) germinate in response to high light and
temperatures, but the germination of seeds of climax species
does not require such conditions (Bazzaz and Pickett 1980,
Brokaw 1985). In addition to germinating in response to
high light and temperatures, seedlings and saplings of
pioneer species grow faster in response to these gap
conditions than the juveniles of climax species (Whitmore
1978 Bazzaz and Pickett 1980, Saulei 1984, Brokaw 1985,
Denslow 1987, Denslow et al 1990). These studies suggested
that the establishment of climax species from seeds may be
rare in gaps because of competition from the fast growing
pioneer species. In support of this hypothesis, most
regeneration of climax species in small to medium gaps is
the result of growth of saplings and poles established prior
to gap formation (Hartshorn 1978, Hubbell & Foster 1986,
Kasenene 1987). Presumably, these size classes are more
competitive than seedlings. However, some studies have
shown that some climax species are capable of germinating
and growing in high-light conditions (Osunkoya 1992).
Furthermore, when small mammals were excluded, some large-
seeded species became established in gaps from seeds (Forget
1991, this study). Therefore, in addition to competition
from pioneer species, and to the low chances of being
dispersed in gaps (Denslow & Diaz 1990), establishment of
large-seeded species in gaps from seeds may also be limited
by seed and seedling predation.

In this study, the number of *Mimusops* seeds that became established seedlings when rodents were excluded was higher in gaps than in the understory in the mature forest compartment. Excluding seeds taken by rodents, 71% (41 seeds) of seeds that died in rodent cages appeared to have succumbed to fungal infection. Seedling establishment of *Mimusops* was even greater in the brighter gaps of the logged forest. The number of *Strombosia* seeds that became seedlings when rodents were excluded did not differ between gaps and understory in both mature and logged forest. These results suggest that in the absence of rodent predation, *Mimusops* would probably establish better in gaps than in the understory, and *Strombosia* may establish equally well in both gaps and in the understory. *Mimusops* seeds are apparently more vulnerable to fungal and pathogen attack in the humid conditions of the understory of a mature forest. Seedling establishment of *Mimusops* was high in the understory of the logged forest. Presumably these sites were less humid. I concur with Sork (1987) that vulnerability of large seeds to mammalian seed predators in gaps may exclude large seeded species from establishing in gaps.

Data from the unprotected seeds are not conclusive; however a higher number of seedlings (5 and 3 for *Strombosia* and *Mimusops*, respectively) established in the understory of the logged forest than in any other habitat type. Only one

Strombosia seed became an established seedling in a gap of
the logged forest. No establishment occurred elsewhere.

The conclusion that seed predation contributes to the
paucity of large seeded species in gaps is also supported by
results from elsewhere. For example, Schupp (1988 b),
working with seeds of *Framea occidentalis* concluded that the
advantages of fast growth in gaps may be counteracted by the
extreme seed and seedling predation in gaps. Working with
seeds of *Welfia georgii*, Schupp & Frost (1989) recorded
lower seed survival in gaps than in the understory. At Los
Tuxtlas, Mexico, Dirzo and Miranda (1990) found unusually
extensive 'carpets' of seedlings and saplings of large-
seeded species on the floor of a defaunated forest. They
attributed the great abundance of these juveniles to the
absence of mammalian seed and seedling predators.

Summary and Conclusions

1) Exclusion of rodents improved seed survival
significantly. Seedling establishment of *Strombosia* was
the same regardless of location (gap or understory, logged
or mature forest) when rodents were excluded. When rodents
were excluded, seedling establishment of *Mimusops* was
higher in gaps than understory of a mature forest. Rodents
probably contribute greatly to the rarity of juveniles of
large-seeded species in gaps.

2) In the logged forest, ground vegetation cover had a
negative effect on seed survival for both *Mimusops* and

Strombosia seeds. Therefore, processes such as logging that encourage the formation of thick ground vegetation cover, may impede the regeneration of large seeded species because they attract rodents that kill seeds and seedlings.

    3) Litter depth influenced seed survival positively, while ground vegetation cover had a negative influence on seed survival. Litter depth was deepest in the understory of forest patches in the logged forest, and ground vegetation cover was lowest in the same habitat type. Furthermore, survival of control seeds was generally higher in understory of forest patches in the logged forest than elsewhere. Therefore, these patches may serve as suitable regeneration centers for large seeded tree species in logged forests.

Table 2-1: Openness, ground vegetation cover (GVC), canopy litter depth, and volume of wood in gaps and understories of a mature forest (K30) and a selectively logged forest (K15) of Kibale Forest Reserve, Uganda. Averages in the rows with the same letter are not significantly different (Scheffe's procedure p < 0.05).

Site mean score

Variable	Mature forest Gap	Mature forest Under-story	Logged forest Gap	Logged forest Under-story	$F_{3,116}$	p
Openness	9.00[b]	1.066[a]	11.95[c]	1.625[a]	88.05	<0.0001
S.D	±4.56	±0.58	±4.24	±0.85		
Range	3-16	0.5-2.5	0.5-16	1.5-3		
GVC (%)	44.8[b]	12.7[a]	83.97[c]	8.066[a]	98.22	<0.0001
S.D	±30.34	±10.93	±20.69	±5.98		
Range	2-95	1-43	13-100	1-23		
Litter depth (cm)	1.39[a]	1.49[a]	1.33[a]	2.05[b]	6.45	=0.0005
S.D	±1.01	±0.51	±0.50	±0.70		
Range	0.1-5	0.5-2.5	0.5-2.3	0.5-3.8		
Volume of wood (m^3)	3.69[b]	0.58[a]	0.103[a]	1.113[a]	8.11	=0.0001
S.D	±5.81	±0.94	±0.33	±1.75		
Range	0-24	0-2.5	0-1.3	0-4.3		

Table 2-2: Average number of days seeds of *Mimusops* survived in control, large mammal exclosures, and rodent exclosures during phase 1 and phase 2 of the experiment. Separate analyses were conducted for gap and understory of the mature forest compartment K30 and of the logged forest compartment K15. Ranges and standard deviations (see Tables A.4 and A.5). Averages in the rows with the same letter are not significantly different (Scheffe's procedure p < 0.05). 1 and 2 stand for the first and second study phases respectively.

Habitat type		Average duration (days)				
	Phase	Control	Large Mammal Exclosures	Rodent Exclosures	$F_{2,87}$	p
Mature forest	1	26.76[a]	22.96[a]	71.76[b]	30.02	<0.0001
Gap	2	47.4[a]	30.86[a]	90.6[b]	36.72	<0.0001
Mature forest	1	19.7[a]	23.06[a]	74.93[b]	51.51	<0.0001
Understory	2	48.46[a]	41.93[a]	87.96[b]	18.74	<0.0001
Logged forest	1	19.9[a]	16.36[a]	77.4[b]	75.96	<0.0001
Gap	2	35.2[a]	21.3[a]	87.8[b]	52.12	<0.0001
Logged forest	1	26.7[a]	28.8[a]	78.8[b]	42.41	<0.0000
Understory	2	62.93[a]	65.87[ab]	86.13[b]	4.47	=0.0141

Table 2-3: Average number of days seeds of *Strombosia* survived in control, large mammal exclosures and rodent exclosures during phase 1 and phase 2 of the experiment. Separate analyses were conducted for gap and understory of the mature forest compartment K30 and for the logged forest compartment K15. Ranges and standard deviations (see Tables A.6 and A.7). Averages in the rows with the same letter are not significantly different (Scheffe's procedure p <0.05). 1 and 2 stand for the first and second study phases respectively.

Habitat type		Average duration (days)				
	Phase	Control	Large Mammal Exclosures	Rodent Exclosures	$F_{2,87}$	p
Mature forest	1	20.8^a	23.66^a	69.26^b	25.37	<0.0001
Gap	2	30.8^a	36.2^a	87.4^b	45.17	<0.0001
Mature forest	1	27.16^a	27.63^a	71.8^b	25.48	<0.0001
Understory	2	49.6^a	52.0^a	78.6^b	9.41	=0.0002
Logged forest	1	28.5^a	26.3^a	86.5^b	61.18	<0.0001
Gap	2	34.20^a	43.7^a	85.8^b	26.79	<0.0001
Logged forest	1	47.16^a	48.7^a	83.2^b	15.71	<0.0001
Understory	2	83.2^b	66.6^a	82.9^b	4.57	=0.0129

Table 2-4: Average number of days survived by *Mimusops* and *Strombosia* seeds in gaps and understory of mature forest compartment (K30) and in gap and understory of a logged forest compartment (K15) during the first and second study phases. Only control seeds were compared. Ranges and standard deviations in (Tables A.4-A.7).

Species		Mature forest Gap	Mature forest- Under- story	Logged forest Gap	Logged forest- Under- story	$F_{3,116}$	p
Mimusops	1	26.77[a]	19.7[a]	19.9[a]	26.7[a]	0.781	=0.506
	2	47.4[ab]	48.47[ab]	35.2[a]	62.9[b]	2.96	=0.035
Strombosia	1	20.86[a]	27.16[a]	28.5[ab]	47.16[b]	5.14	=0.002
	2	30.8[a]	49.6[a]	34.2[a]	83.2[b]	23.19	<0.001

Averages in the rows with the same letter are not significantly different (Scheffe's procedure p =0.05). 1 and 2 stand for the first and second study phases respectively.

Table 2-5: Significant results of the logistic regression of probability of *Mimusops* and *Strombosia* seeds being present at the final census, 95 days, against canopy openness, ground vegetation cover (GVC), litter depth and volume of wood in mature and logged forest compartments. Significant results were obtained only in the logged forest compartment in the second phase.

Species		Regression type	Significant Variable	Wald	R	p
Mimusops	(2)	Stepwise	GVC	9.33	[-]0.316	=0.0023
Mimusops	(2)	Simple	Openness*	8.39	[-]0.30	=0.0038
Strombosia	(2)	Stepwise	GVC	11.6	[-]0.349	=0.0007
Strombosia	(2)	Simple	Openness*	9.51	[-]0.309	=0.002
Strombosia	(2)	Simple	Litter depth*	7.07	[+]0.254	=0.0078

* Designates variables that were not included as significant in the stepwise regressions but were significant if regressed separately.

Table 2-6: The fate of 120 seeds of *Mimusops* in four
habitat types, understory and gaps of the mature forest
compartment K30, and understory and gaps of the logged
forest compartment K15, 241 days from the start of the
second study phase. The experiment involved three
treatments: control, large mammal exclosure, and rodent
exclosure.

Habitat type	Fate	Control	Large Mammal Exclosure	Rodent Exclosures
Mature forest understory	Seedlings	00	00	04
	Seeds	00	00	00
	Rotten	00	00	18
	Eaten	25	26	04
	Unknown	05	04	04
	Total	30	30	30
Mature forest gap	Seedlings	00	00	12
	Seeds	00	00	00
	Rotten	00	00	08
	Eaten	23	29	06
	Unknown	07	01	04
	Total	30	30	30
Logged forest understory	Seedlings	03	03	13
	Seeds	00	00	00
	Rotten	00	01	10
	Eaten	16	18	05
	Unknown	11	08	02
	Total	30	30	30
Logged forest gap	Seedling	00	00	13
	Seeds	00	00	00
	Rotten	00	00	05
	Eaten	27	30	05
	Unknown	03	00	07
	Total	30	30	30

Table 2-7: The fate of 120 seeds of *Strombosia* in four
habitat types, understory and gaps of the mature forest
compartment K30, and understory and gaps of the logged
forest compartment K15, 241 days from the start of the
second study phase. The experiment involved three
treatments: control, large mammal exclosure, and rodent
exclosure.

Habitat type	Fate	Control	Large Mammal Exclosures	Rodent Exclosures
Mature forest understory	Seedlings	00	01	12
	Seeds	00	00	00
	Rotten	00	00	08
	Eaten	30	26	02
	Unknown	00	03	08
	Total	30	30	30
Mature forest gap	Seedlings	00	01	14
	Seeds	00	00	00
	Rotten	00	02	08
	Eaten	30	27	02
	Unknown	00	00	06
	Total	30	30	30
Logged forest understory	Seedlings	05	05	12
	Seeds	00	00	00
	Rotten	00	04	07
	Eaten	13	11	04
	Unknown	12	10	07
	Total	30	30	30
Logged forest gap	Seedling	01	02	15
	Seeds	00	00	03
	Rotten	01	01	04
	Eaten	28	27	04
	Unknown	00	00	04
	Total	30	30	30
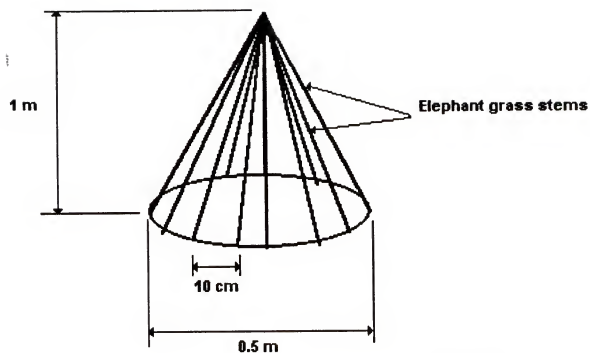
Figure 2-1: Sketch of the large mammal exclosure, showing height, diameter, and spaces between elephant grass stems.

CHAPTER 3

SEEDLING PREDATION IN MATURE AND LOGGED FOREST
COMPARTMENTS

Introduction

Canopy gaps play an important role in the
regeneration of most tropical forest trees (Schulz 1960,
Whitmore 1975, 1978, Denslow 1978, 1980, Gelmond 1978,
Hartshorn 1978, 1989, Brokaw 1985). Physiological studies
have shown that seeds of small-seeded (pioneer) trees
germinate and grow faster in response to light gaps than
large-seeded (climax) species (Whitmore 1975, 1978, Bazzaz
and Pickett 1980 Brokaw 1985, Hubbell & Foster 1986).
This difference in response to light may explain why
large-seeded species are rare in gaps (Whitmore 1975,
1978, Bazzaz and Pickett 1980 Brokaw 1985, Hubbell &
Foster 1986). From a pathological view point, Augspurger
(1984) and Augspurger & Kelly (1984) demonstrated that
seedlings growing in gaps were less prone to pathogens
than those growing in the understory.

Mammalian seed and seedling predators appear to be
important in gap regeneration dynamics (e.g., Hartshorn
1978, Sork 1978, Schupp 1988 a, b, 1990, Schupp et al.
1989, Schupp and Frost 1989, Turner 1990). Some field
studies (Sork 1987, Forget 1991) have shown that seedlings
of some large-seeded tree species classified as non-

pioneer species (Bazzaz & Pickett 1980, Swaine and Whitmore 1988, Brown 1993) can actually become established in gaps if seed and seedling predators are excluded.

According to the escape hypothesis (Howe and Smallwood 1982), seedlings beneath parent trees suffer disproportionately higher mortality than those further away from parents. In gaps, seedlings of climax species will definitely be isolated from parents. Thus, according the escape hypothesis, seedlings in gaps should suffer less mortality than those in the understory. Seedling density of climax species is likely to be lowest in gaps, particularly in large gaps such as those created by mechanical logging, unless seedlings were present prior to gap formation. Using this argument, Hartshorn (1978) predicted higher survival of seedlings of climax species in gaps than in the understory.

Several studies have been conducted to test this prediction, but results are far from consistent. In some studies, seedling survival was greater in gaps than in the understory (De Steven & Putz 1984, Webb & Willson 1985, Sork 1987, Myster & McCarthy 1989, Turner 1990, Forget 1991). In contrast, Forget (1991), and Webb and Willson (1985) reported no difference, while Schupp (1988 a, b) and Schupp & Frost (1989) reported lower seedling survival in gaps than in the understory. In all these studies rodents were implicated in seedling mortality. Inconsistency was presumably due to differences in

geographic regions, differences in palatability of seedling species, and annual variation in alternative foods and predator abundance.

Despite the inconsistencies in previous studies, the hypothesis that seedlings in gaps are more vulnerable to predation than those in the understory seems plausible based on results from studies of small mammal (seedling predator) populations (see below). The association of small mammals with dense vegetation such as that found in gaps has been observed by several authors (e.g., Rood and Test 1968, Janzen 1970, 1971, Delany 1971, Synnott 1975, Emmons 1982, Kasenene 1984, Isabirye-Basuta & Kasenene 1987, Muganga 1989, Walker & Rabinowitz 1992). Also, several studies on the ecology of large seeds and their seedlings have demonstrated that rodents are the most important cause of seed and seedling mortality (Janzen 1969, Harper 1977, Howe and Richter 1982, Sork 1987, Schupp 1988 a, b, Forget 1991, Myster & McCarthy 1989, Turner 1990).

Based on the preceding findings, I hypothesized that seedling predation would be higher in a logged forest than in a mature forest, because ground vegetation cover is more dense in the former. I further hypothesized that seedling predation should be higher in gaps than in the understory in both forests.

In addition to studying seedling predation, I examined the impact of insect browsers on seedlings in

gaps and understory of logged and mature forests. A study
of arthropod populations in Kibale Forest reported no
differences in arthropod numbers between logged and mature
forest compartments (Nummelin 1989). However, when
Nummelin's (1989) data were reanalysed, the logged forest
had significantly more arthropods than the mature forest
(Tom Struhsaker pers. comm). Based on these results, it
was hypothesized that the extent of leaf damage caused by
insects on experimental seedlings is greater in the logged
forest than in the mature forest.

This study also examined differences in height
growth-increments between gap and understory seedlings in
both logged and unlogged compartments. Seedlings of two
large-seeded species *Mimusops bagshawei* and *Strombosia
scheffleri* were used.

Objectives:

This study tested for differences in seedling
survival between logged and mature forest compartments and
between gaps and understory. Previous rodent studies in
Kibale (Kasenene 1984, Isabirye-Basuta & Kasenene 1987,
Muganga 1989) indicated higher rodent abundance in logged
forest compartments than in the mature forest compartment.
They also indicated positive correlations between rodents
abundance and thick ground vegetation cover, such as that
found in gaps. Thus I predicted that:

1) Seedling survival should be higher in the mature forest than in the logged forest.

2) Seedling survival should be higher in the understory than in gaps.

3) Insect leaf damage should be greater in the logged forest than in the mature forest, and greater in gaps than in the understory.

4) Height growth-increments should be greater in gaps than in the understory.

Methods and Materials

Raising of Seedlings

A nursery bed, 1.5 m wide and 2.5 m long, was raised 1 m from the ground and filled with forest soil. The nursery was enclosed in a wire mesh (2mm X 2mm) to exclude large insects and rodents. A shelter of elephant grass, was constructed above to mimic light conditions of the forest floor and to reduce desiccation. Six hundred *Strombosia* seeds were planted on the soil surface on October 23, 1992. Seeds were watered in the morning and in the evening whenever it did not rain. October through November and March through May were wet months. Germination was first observed on November 17,1992. Of the 600 seeds sown, 473 (78.8%) germinated. Seeds and seedlings that were attacked by fungi were removed from the nursery as soon as they were detected to prevent

spread of fungi. Seedlings were transplanted into plastic bags two weeks prior to being planted in the forest. Only healthy seedlings were planted in the forest.

The germination rate of *Mimusops* seeds was very low; thus several germination trials were made in order to raise a reasonable number of seedlings. Germination trials were made in the nursery, in petri dishes, and in chimpanzee dung. Rates of germination were 13% (n = 600 seeds) and 31% (n = 367 seeds) for seeds planted in the nursery and chimpanzee dung, respectively. None of the 350 seeds planted in petri dishes germinated. Seeds collected from the forest and sown in chimpanzee dung on July 7, 1992, started to germinate on September 5 1992. Another group of seeds was sown in chimpanzee dung on October 23 1992, and germination started during the second week of December 1992. A few seedlings germinated in March 1993, from seeds that were sown in the nursery on October 23, 1992. Seeds that sprouted in chimpanzee dung were transplanted into plastic cups and then transferred to the seedling house where they were watered regularly.

Experimental Design and Monitoring

The experiment was conducted in the same locations as the seed predation experiment (see Chapter 2). Seedlings were planted in the forest during the wet season to avoid the problem of watering.

Sixty *Strombosia* and 60 *Mimusops* seedlings were planted in the logged forest on February 25 and 26 1993, respectively. These seedlings were planted in thirty forest patches and 30 corresponding gap locations. One seedling of each species was planted in the center of each forest patch. Another pair of seedlings (one of each species) was planted approximately 20 m away from the edge of the patch into a gap opened by logging. Seedlings were removed from the plastic containers before they were planted. Heights were measured with a ruler two days after planting and at final census to determine growth in height. Leaf margins were traced on paper before seedlings were planted. At the end of the experiment, leaf damage was estimated by comparing leaf size at final census with size of the trace at planting. Five percent class intervals were used.

In the mature forest, *Strombosia* seedlings were planted on February 27 1993, and *Mimusops* seedlings were planted on May 5 1993, when enough seedlings had been acquired. The thirty gaps and corresponding locations in the understory used in the seed predation experiment were also used in this experiment. One seedling of each species was planted approximately in the center of each gap. Approximately 20 m away from the edge of the gap, another pair of seedlings was planted in the understory. Heights of seedlings were measured two days after planting.

Seedlings were monitored once a week for the first two months. Thereafter, they were monitored once a month. During each visit, seedlings were classified as alive and stem intact, alive with stem damage, or dead. Cause of stem damage and death were evaluated from tooth marks on stems. Leaf damage was expressed as proportion of leaf eaten. Fungal infection was also noted.

Date of predation was estimated as mid-way between the day when the seedling was previously observed and the day when it was found dead or with a gnawed stem.

Estimation of Environmental Variables at Seedling Stations

The experiment was performed in the same locations as the seed predation experiment; thus the previous measures of ground vegetation cover, litter depth, and volume of wood (Chapter 2) were used. During the last week of the experiment, light conditions at all surviving *Strombosia* seedlings was estimated using ozalid paper (Friend 1961). *Strombosia* seedlings were chosen because they exhibited appreciable height increments during the course of the experiment. Nine sheets of ozalid paper (2.5 cm X 2.5 cm) were piled together and enclosed in a manila jacket with a hole (0.5 cm diameter) in the center to allow light to enter. One pile of ozalid paper covered in a pair of petri dishes (to protect against rain) was placed near the base of each surviving *Strombosia* seedling and left in the

field. After a week, the number of sheets that had changed color in each pile was counted. Sheets that had barely changed were given a score of 0.25, and those between the original color and fully changed were given a score of 0.5. The number of sheets that change color is proportional to light intensity (Friend 1961).

Statistical Analysis

Differences in number of days survived by *Mimusops* and *Strombosia* seedlings among the four habitat types (i.e., gaps and understory of mature forest and gaps and understory of logged forest) were tested using the one-way ANOVA. Scheffe's procedure ($p < 0.05$) was employed to test for differences between any two habitat types in all possible pair combinations.

Observations on *Strombosia* seedlings lasted 122 days in both forest compartments, and differences in seedling survival among the four habitat types were performed on the same day. Observations on *Mimusops* seedlings lasted 122 days in the logged forest, and 62 days in the mature forest. For this reason, differences in seedling survival among the four habitat types were tested on day 62.

The 2 X 2 G-test (Sokal & Rohlf 1969) was employed to test for differences in number of *Mimusops* and *Strombosia* seedlings that survived to final census among the four habitat types in pair combinations.

The logistic regression (Trexler & Travis 1993) was employed to examine the relationship between probability of a seedling surviving up to final census and canopy openness, ground vegetation cover, litter depth, and volume of wood in the vicinity of the seedling. Analysis was performed on day 62 for *Mimusops* seedlings in the mature forest. For *Strombosia* seedlings as well as *Mimusops* seedlings in the logged forest, analysis was performed after 122 days. Three analyses, simple logistic regression, multiple regression, and stepwise regression were conducted.

Results

Causes of Seedling Mortality

One hundred and twenty *Strombosia* seedlings were planted (average diameter at time of planting 0.45 cm range = 0.29 - 0.56 cm, average height = 12.3 cm, range = 8.5 - 16 cm). Forty-eight seedlings died during the observation period. Judging from tooth marks on remains of dead seedlings and from dung that was sometimes found on sites where seedlings had been killed, 45 *Strombosia* seedlings were killed by rodents. Not all stem damage inflicted by rodents on stems of *Strombosia* seedlings was fatal. Sometimes rodents ate small bits of the stems without killing the seedlings. One seedling in the understory of the logged forest died from fungal attack. In the mature forest, one seedling planted in the

understory, subsequently died after being infected by
fungi in wounds inflicted by a rodent on the stem. Two
seedlings in gaps of the mature forest were trampled and
killed by elephants.

Of the 120 *Mimusops* seedlings (average diameter at
time of planting = 0.11 cm, range = 0.08 - 0.13 cm,
average height = 6.2 cm, range = 3 - 8.9 cm), that were
planted, 44 died during the course of the experiment.
Browsing on stems of *Mimusops* seedlings was always fatal.
Sometimes cotyledonous leaves were also consumed. Debris,
and in two cases, rodent dung found at sites where
seedlings had been eaten suggest that seedlings were
killed by rodents. No other cause of death of *Mimusops*
seedlings was observed during the course of the
experiment.

Survival of *Mimusops* and *Strombosia* Seedlings in Gaps and Understory of Mature and Logged forests

For *Mimusops*, comparisons between compartments were
performed on day 62 (i.e., maximum longevity in the mature
forest was taken to be 62 days) although observations
lasted 122 days in the logged forest. The number of days
Mimusops seedlings survived, differed significantly among
gaps and understory of the mature and logged forests
(Table 3-1 and Table A.8). Average seedling survival was
longest in the understory of the logged forest. Average
number of days survived by *Mimusops* seedlings in the

understory of the logged forest was significantly longer than in gaps of the same forest. Differences in seedling survival among understory of the logged forest, understory of the mature forest, and gaps of the mature forest were not significant (Table 3 -1).

In the logged forest, 11 seedlings (36.7%) and 25 seedlings (83.3%) of *Mimusops* survived in gaps and understory, respectively for at least 122 days. Average number of days *Mimusops* seedlings survived in the understory (107.4 days) was significantly longer than in gaps (59.9 days) (t = 4.229, df = 58 p < 0.001).

For *Strombosia*, differences in seedling survival among the four habitat types were tested on day 122. Two types of browsing on stems of *Strombosia* seedlings were observed; fatal, and non-fatal (at least during the study period). The numbers of *Strombosia* seedlings that were alive at the final census were 22, 26, 10, and 14, in gaps and understory of logged forest, and in gaps and understory of mature forest respectively. Of the 22 seedlings that were alive in gaps of the logged forest, 14 had gnawed stems, and 12 of the 26 seedlings that were alive in the understory of logged forest had gnawed stems. In gaps of the mature forest, of the 10 seedlings that were alive 8 stems were gnawed, and in the understory, of the 14 seedlings that were alive 9 had gnawed stems.

Considering all seedlings that were alive at final census (including those with damaged stems), the number of

days *Strombosia* seedlings survived differed significantly among habitat types (Table 3-1 and Table A.8). Pairwise comparisons indicated that seedlings in the understory of the logged forest survived significantly longer than those planted in gaps and understory of the mature forest (Table 3-1). Seedlings planted in gaps of the logged forest survived longer than those in gaps of the mature forest. No difference was detected between number of days seedlings survived in gaps of logged forest and in understory of mature forest. Differences between number of days *Strombosia* seedlings survived in gaps and understory of the same forest did not differ (Table 3-1).

When seedlings with gnawed stems were excluded from the analysis (i.e., survival taken to be equal to number of days before stem was damaged), mean number of days survived was shorter but trends and levels of significance were the same as above (Table 3-1).

Survival at Final Census

In the logged forest, a significantly higher proportion of *Mimusops* seedlings survived in the understory than in gaps (Table 3-2), and this trend was consistent throughout the study period. In the mature forest, there was no difference between number of *Mimusops* seedlings that survived in the understory and in gaps (Table 3-2). Survival of *Mimusops* seedlings did not differ between understory of the mature forest and

understory of the logged forest. Survival of *Mimusops* seedlings in gaps of the mature forest was marginally higher than in gaps of the logged forest. There was no difference between number of *Mimusops* seedlings that survived in the logged and in the mature forest compartments (Table 3-2).

For *Strombosia* in the logged forest, the number of live seedlings with no stem damage (i.e., when live seedlings with damaged stems were counted as doomed) was slightly higher in the understory than in gaps, but this difference was marginally significant (Table 3-3). The number of seedlings surviving regardless of stem damage (i.e., live seedlings with damaged seedlings counted as alive) did not differ significantly between gaps and understory of the logged forest (Table 3-4). In the mature forest, results were similar to those in the logged forest. No significant differences were found between number of *Strombosia* seedlings with no stem damage in the gaps and in the understory (Table 3-3). When seedlings with stem damages were counted as alive (Table 3-4), the difference between number of seedlings that survived in gaps and in the understory of the mature forest was also not significant.

Comparisons between logged and mature forest revealed significant differences (Tables 3-3 and 3-4). The number of live *Strombosia* seedlings, with no stem damage, was significantly higher in the understory of the logged

forest than in the understory of the mature forest (Table 3-3). When all live seedlings (including those with stem damage) were included in the analysis, this difference was less significant (Table 3-4). One seedling in the understory of the logged forest died from fungal attack. Therefore only three seedlings actually died as a result of predation in the understory of the logged forest compared to 16 that died in the understory of the mature forest (Table 3-4). A similar trend was observed when gaps of mature and logged forests were compared. Number of *Strombosia* seedlings with no stem damage was marginally significantly higher in gaps of the logged forest than in gaps of the mature forest (Table 3-3). Similarly, when stem damage was disregarded, significantly more seedlings were alive at final census in gaps of the logged forest than in gaps of the mature forest (Table 3-4). Overall, the number of *Strombosia* seedlings that incurred no stem damage was significantly higher in the logged forest than in the mature forest. Comparable results were obtained when stem damage was disregarded and number of all live seedlings was considered. A significantly higher number of seedlings were alive at final census in the logged forest than in the mature forest (Table 3-4). These results were contrary to what was predicted but were consistent with rodent populations in the two forests (see Chapter 4).

Habitat Characteristics That Influence the Probability of Seedling Survival in Logged and Mature Forests

In the mature forest, none of the habitat variables was related to the probability of being alive at final census for *Mimusops* seedlings in all three analyses (Table 3-5). In the logged forest, the probability of *Mimusops* seedlings being alive at final census was negatively related to canopy openness and ground vegetation cover in the simple logistic regression (Table 3-5). In the multiple regression, none of the habitat variables was significantly related to seedling survival. However, in the stepwise regression, ground vegetation cover was significantly negatively related to probability of seedlings being present at final census. Canopy openness was not related to seedling survival in this analysis, but this is because canopy openness and ground cover were correlated ($r = {}^+0.837$, $p < 0.0001$, $df = 118$). Hence the two explained the same variance.

For *Strombosia* seedlings in the mature forest, the simple logistic regression revealed a weakly negative relationship between the probability of a seedling's presence at final census and ground vegetation cover (Table 3-5). In the same analysis, there was a strong positive relationship between probability of *Strombosia* seedlings being present at final census and litter depth. This relationship was also significant in the multiple and stepwise regression (Table 3-5).

In the logged forest, the simple logistic regression revealed a negative, but weak relationship between ground vegetation cover and probability of presence of *Strombosia* seedlings at final census (Table 3-5) In the multiple regression, the probability of seedlings being present was negatively correlated to ground vegetation cover, and positively correlated to canopy openness. In the stepwise regression, none of the habitat variables was significantly related to probability of final survival of *Strombosia* seedlings in the logged forest.

Levels of Insect Damage on Seedling Leaves

Leaf damage on cotyledonous leaves of experimental seedlings that survived to the final census was expressed as percentage of each leaf consumed, and the average was recorded. The nature of the damage and other indicators, i.e., holes, irregular cuttings on leaf margins and sometimes inch-worms and caterpillars found on damaged leaves, suggested that damage was caused by insects. Average insect leaf damage on leaves of *Mimusops* was: $1.63\% \pm 5.43\%$, $5.52\% \pm 16.24\%$, $6.35\% \pm 16.93\%$, and $6.57\% \pm 23.5\%$ in gaps of the logged forest, understory of the logged forest, gaps of the mature forest and understory of the mature forest, respectively. However, one-way ANOVA on arcsine of percent leaf damage did not reveal significant differences in insect browsing among gaps and

understory of logged and mature forests ($F_{3,71}$, = 0.223, p = 0.8799).

Insect leaf damage on *Strombosia* seedlings was lowest in gaps of the logged forest (4.41% $\pm$ 9.53%) followed by understory of the logged forest (11.65% $\pm$ 21.30%), and understory of the mature forest (42.71% $\pm$ 35.55%), and was highest in gaps of the mature forest (51.5% $\pm$ 31.02%). Analysis of variance on arcsine of percent leaf damage ($F_{3,68}$ = 10.7, p <0.0001) indicated that differences between gaps and understory within the same forest compartment were not different. But leaf damage in gaps and understory of logged forest were significantly lower than leaf damage in gaps and understory of the mature forest (Scheffe's procedure p < 0.05). In the mature forest, caterpillars and inch-worms were frequently found on damaged leaves of *Strombosia*.

Differences in Seedling Growth Rates Among Habitat Types

Growth in height of *Mimusops* seedlings was negligible. In several cases, rain water deposited soil at the base of the seedling, and negative growth was recorded at final census for some seedlings. Therefore, comparisons of growth among habitat types were not performed for *Mimusops*.

There were appreciable increments in height of *Strombosia* seedlings over the study period (122 days), and growth differed significantly among the four habitat types

($F_{3,68}$ = 3.35, p = 0.0239). Growth was least in gaps of the mature forest (average = 0.53 cm, range 0 - 0.7 cm, N = 10), followed by growth in the understory of mature forest (average = 1.05 cm, range = 0.1 - 2.5 cm, N = 14), and by growth in the understory of the logged forest (average = 1.44 cm, range = 0 - 4.1 cm, N = 26). Growth in height was greatest in gaps of the logged forest (average = 2.33 cm, range 0 - 9.4 cm N = 22). Scheffe's procedure (p < 0.1) indicated that the only significant difference in growth was between gaps of the logged forest and gaps of the mature forest.

Correlates of *Strombosia* Seedling Growth: Logged and Mature Forest Combined

The relationships between seedling growth and light, leaf damage (arcsine of percent), ground vegetation cover, and litter depth were examined using multiple regression. Thirty-four percent of the variance in growth was explained by the regression (R = 0.348, $F_{4,67}$ = 2.317, p =0.066). Partial correlation analyses were employed to determine the relationships between each independent variable and seedling growth when the linear effects of the other variables were controlled. When linear effects of other variables were removed, leaf damage was marginally negatively correlated with seedling growth (partial r = ⁻0.22, p = 0.066). The correlations of litter depth (partial r = ⁻0.0186, p = 0.879), light

(partial r = 0.182, p = 0.133), ground vegetation cover
(partial r = 0.056, p = 0.645) were not significant.

This suggests that leaf damage and possibly light
were the most important variables influencing growth rates
of *Strombosia* seedlings. Accordingly, the relationships
between these variables and seedling growth were tested.
Thirty-four percent of the variance in growth was
explained by the regression of growth with light and leaf
damage (R = 0.3429, $F_{2,69}$, = 4.597, p = 0.013). When the
linear effects of light were removed, leaf damage was
marginally negatively correlated with growth (partial r =
$^-$0.2377, p = 0.053). And when the linear effects of leaf
damage were removed, light was positively correlated with
growth (partial r = 0. 254, p = 0.032).

Discussion

Seedling Survival in Gaps and Understory of Mature and Logged Forests

Results from this study, like those from elsewhere
(see Schupp & Frost 1989), were not consistent. Survival
of *Mimusops* seedlings, based on average number of days
survived by seedlings (Table 3-1), as well as on number of
seedlings that survived to final census (Table 3-2), was
higher in the understory than in gaps in the logged
forest. This trend was consistent with my prediction. In
the mature forest, survival of *Mimusops* seedlings did not
differ between gaps and understory. The prediction that

seedling survival should be higher in the mature forest
than in logged forest was not supported by data from
Mimusops seedlings. There was no difference in seedling
survival between logged and mature forest as was predicted
basing on reports that rodent density was higher in logged
than in mature forests (Kasenene 1984, Isabirye-Basuta &
Kasenene 1987, Muganga 1989)..

Data collected on *Strombosia* seedlings also did not
support the prediction that seedling survival is higher in
the understory than in gaps. The prediction that seedling
survival is higher in the mature forest than in the logged
forest was also not supported by data collected on
Strombosia seedlings. To the contrary, seedling survival
was significantly higher in the logged forest than in the
mature forest (Tables 3-3 and 3-4). Although this trend
was opposite to what was predicted according to previous
rodent studies in Kibale (Kasenene 1984, Isabirye-Basuta
and Kasenene 1987, Muganga 1989), it was concordant with
rodent populations during the present study (see Chapter
4). Seedling predation was high in the mature forest
where rodent abundance was also high.

As has been the case in a few other studies (Schupp
1988, a, b, Schupp and Frost 1989), differences in
seedling survival between gaps and understory (except for
Mimusops in the logged forest), were not established in
this study. However, logistic regression analyses
indicated that ground vegetation cover increased the

probability of being eaten by rodents for *Strombosia* seedlings in both forest types, and *Mimusops* seedlings in the logged forest. This observation suggests that thick ground vegetation cover renders seedlings vulnerable to predation, and thus may retard forest regeneration.

The Importance of Seedling Predators on Forest Composition

In this study, 44 (36.8%) seedlings of *Mimusops* and 45 (37.8%) seedlings of *Strombosia* died as a result of predation by rodents. Only two (1.7%) *Strombosia* seedlings were trampled by elephants. These observations suggest that the abundance of *Mimusops* and *Strombosia* seedlings is to a great extent determined by browsing by rodents. Dispersal into gaps did not increase survival as predicted by the escape hypothesis (Hartshorn 1978, Howe & Smallwood 1982). Seedling survival was apparently related to rodent density (see Chapter 4). Therefore, high rodent populations can retard the regeneration of preferred plant-food species and hence maintain the plants at lower densities. In Central American forests, where mammalian seed and seedling predators are rare or absent, a few plants species tend to dominate, whereas in forests where seed and seedling predators are abundant the same plant species occur at low densities (De Steven and Putz 1984, Dirzo and Miranda 1990, Leigh et al. 1993). It was concluded that, in old growth forest, seedling establishment was determined mainly by seedling predators

(Myster & McCarthy 1989). These observations further strengthen the assertion that seedling survival is greatly influenced by the abundance of seed and seedling predators. Similar conclusions have been reached from other studies (Buss 1986, Huntly 1991, Osunkoya 1992).

Conclusions

1) The prediction that seedling survival is higher in the understory than in gaps was supported by data collected on *Mimusops* seedlings in the logged forest only. For *Strombosia* seedlings in both forest types, and *Mimusops* seedlings in the mature forest the prediction was not supported. It is therefore concluded that seedling survival between gaps and understory, in general, is difficult to predict, because it varies with seedling species and forest type.

2) All the 46 seedlings of *Mimusops*, and 45 of 47 *Strombosia* seedlings that died during this experiment were killed by rodents. It was concluded that rodents are a major cause of seedling mortality in tropical forests, and can impair forest regeneration at high population densities.

3) A larger proportion of *Strombosia* seedlings survived in the logged forest than in the mature forest, contrary to what was predicted basing on previous reports on rodent populations in the two forest types. However, the population of seedling eating rodents (Chapter 4) was

higher in the mature forest than in the logged forest. It is therefore concluded that *Strombosia* seedling mortality is high where rodent populations are high.

Table 3-1: Average number of days *Mimusops* and *Strombosia* seedlings survived in gaps and in understory of mature forest (K30) and logged forest (K15). For *Mimusops*, differences were tested at day 62 and they were tested at day 122 for *Strombosia*.

Average duration (days)

Species	Mature forest gap	Mature forest understory	Logged forest gap	Logged forest understory	$F_{3,116}$	p
Mimusops						
Average	50.9^{ab}	44.13^{ab}	37.4^{a}	57.36^{b}	5.045	=0.0025
SD	18.5	25.06	24.49	13.53		
Range	1 - 62	1 - 62	1 - 62	1 - 62		
Strombosia[@]						
Average	23.43^{a}	37.77^{ab}	58.97^{bc}	81.4^{c}	10.9	=0.0001
SD	32.92	44.61	45.97	43.25		
Range	1 - 124	1 - 124	1 - 124	1 - 124		
Strombosia[*]						
Average	56.23^{a}	70.46^{ab}	101.2^{bc}	111.82^{c}	10.82	=0.0001
SD	50.54	56.14	36.57	27.62		
Range	1 - 124	1 - 124	1 - 124	1 -124		

Row averages with the same letter are not significantly different, Schefe's procedure (p < 0.05).
[@] Designates averages when live seedlings with damaged stems were counted as doomed.
[*] Designates averages when seedlings with damaged stems were counted as alive.

Table 3-2: Final survival (survival at final census) of
Mimusops seedlings in gaps and understory of mature forest
(K30) and in gaps and understory of the logged forest (K15).
Comparisons involving K30 were performed at day 62, and for
K15 they were performed at day 122.

Habitat types compared	Number surviving	Number planted	G	p	df
Logged forest					
Gap	11	30			
Understory	25	30	12.3	<0.001	1
Mature forest					
Gap	21	30			
Understory	19	30	0.075	>0.1	1
Understory					
Mature forest	19	30			
Logged forest	25	30	2.16	>0.1	1
Gap					
Mature forest	21	30			
Logged forest	11	30	2.75	<0.1	1
Overall					
Mature forest	40	60			
Logged forest	36	60	0.32	>0.1	1

Table 3-3: Number of *Strombosia* seedlings that incurred no
stem damage at final census in gaps and understory of mature
forest (K30) and in gaps and understory of the logged forest
(K15). Analysis was done at day 122.

Habitat types compared	Number with intact stems	Number planted	G	p	df
Logged forest					
Gap	8	30			
Understory	15	29	2.94	<0.1	1
Mature forest					
Gap	2	30			
Understory	5	30	1.50	>0.1	1
Understory					
Mature forest	5	30			
Logged forest	15	29	6.78	<0.01	1
Gap					
Mature forest	2	30			
Logged forest	8	30	3.11	<0.1	1
Overall					
Mature forest	7	60			
Logged forest	23	59	10.73	<0.01	1

Table 3-4: Number of *Strombosia* seedlings that survived at final census (seedlings with damaged stems are counted as alive) in gaps and understory of mature forest (K30) and in gaps and understory of the logged forest (K15).

Habitat type compared	Number surviving	Number planted	G	p	df
Logged forest					
Gap	22	30			
Understory	26	29	1.66	>0.1	1
Mature forest					
Gap	10	30			
Understory	14	30	0.63	>0.1	1
Understory					
Mature forest	14	30			
Logged forest	26	29	5.62	<0.02	1
Gap					
Mature forest	10	30			
Logged forest	22	30	8.3	<0.01	1
Overall					
Mature forest	24	60			
Logged forest	48	59	10.16	<0.01	1

Table 3-5: Results of logistic regression of probability of *Mimusops* and *Strombosia* seedlings being present at final census (62 days for *Mimusops* in the mature forest, 122 days for the rest) against canopy openness, ground vegetation cover GVC, litter depth, and volume of wood in the mature and logged forests.

Species + Forest	Variable	Simple regression p =	Simple regression R =	Multiple regression p =	Multiple regression R =	Stepwise regression p =	Stepwise regression R =
Mimusops Mature forest	Openness	0.492	0.000	0.327	0.000	0.490	0.000
	GVC	0.937	0.000	0.462	0.000	0.937	0.000
	Litter	0.479	0.000	0.455	0.000	0.474	0.000
	Wood	0.719	0.000	0.716	0.000	0.717	0.000
Mimusops Logged forest	Openness	0.007*	-0.245	0.965	0.000	0.936	0.000
	GVC	0.004*	-0.279	0.399	0.000	0.004*	-0.279
	Litter	0.213	-0.000	0.991	0.000	0.981	0.000
	Wood	0.090	+0.104	0.235	0.000	0.186	0.000
Strombosia Mature forest	Openness	0.222	0.000	0.428	0.000	0.086	-0.142
	GVC	0.075	-0.158	0.371	0.000	0.103	-0.119
	Litter	0.016*	+0.283	0.035*	+0.228	0.016*	+0.283
	Wood	0.868	0.000	0.971	0.000	0.694	0.000
Strombosia logged forest	Openness	0.469	0.000	0.039*	+0.169	0.468	0.000
	GVC	0.126	-0.065	0.022*	-0.202	0.123	-0.070
	Litter	0.139	+0.049	0.313	0.000	0.130	+0.062
	Wood	0.638	0.000	0.305	0.000	0.636	0.000

CHAPTER 4

RODENT POPULATIONS IN GAPS AND UNDERSTORY OF MATURE AND
LOGGED FORESTS

Introduction

Rodents are an integral component of tropical rain
forests (Fleming 1975). Their role as seed and seedling
predators has been reported widely (Synnott 1975, Janzen
1969, 1970, 1971, Bradford & Smith 1977, Jeffrey 1977,
Isabirye-Basuta 1979, Kasenene 1984, Mittelbach & Gross
1984, De Steven & Putz 1984, Howe et al. 1985, Webb &
Willson 1985, Sork 1987, Schupp 1988 a, b, 1990, Myster &
McCarthy 1989. Schupp et al. 1989, Whelan et al. 1990,
Turner 1990, Forget 1991, 1993). However, rodents also
scatter-hoard seeds, and if they fail to return to the
hoard, and if it is in a location suitable for germination
and growth, rodents can act as secondary seed dispersers
(Janzen 1971, Hallwachs 1986, Forget 1991, 1993).

Rodents often live in dense vegetation, such as that
found in gaps created by logging (Rood and Test 1968, Janzen
1970, 1971, Delany 1971, Synnott 1975, Emmons 1982, Kasenene
1984, Isabirye-Basuta & Kasenene 1987, Muganga 1989, Walker
& Rabinowitz 1992). Therefore, it may not be surprising
that long-term studies of small rodents in Kibale Forest,
Uganda, concluded that rodent densities and species
diversity were higher in logged forests than mature forests

(Kasenene 1984, Isabirye-Basuta & Kasenene 1987, Muganga 1989). These studies suggest that regeneration of large seeded tree species is hampered more severely by rodents in logged than in mature forests.

Based on these previous studies, I predicted that seed predation (Chapter 2) and seedling predation (Chapter 3) would be higher in logged forests than in mature forests. However, I found that seed survival in the logged forest was equal to or higher than seed survival in the mature forest (Chapter 2). It was also determined that there was no difference in the survival of *Mimusops* seedlings between logged and mature forests; and that survival of *Strombosia* seedlings was sometimes higher in the logged forest than in the mature forest (Chapter 3). These findings would suggest that unlike previous studies (Kasenene 1984, Isabirye-Basuta & Kasenene 1987, Muganga 1989), rodents were more abundant in the mature forest than in the logged forest during this study. Rodent trapping was, therefore, conducted for four months to examine this possibility. The hypothesis that rodents are more abundant in gaps than understory (Schupp 1988 a) was also examined.

Methods

Rodent Trapping

The 10 largest gaps, ranging in size from 213 m^2 - 823 m^2, of the 30 gaps used in the seed and seedling predation experiments in the mature forest were selected for rodent

trapping. Ten Sherman live traps, baited with a fermented mixture of ripe sweet bananas (60% by weight), maize flour (30%), and roasted and pounded ground nuts (10%) (Isabirye-Basuta 1979, Kasenene 1984, Muganga 1989) were set in each of the 10 gaps. Identical bait was used to ensure compatibility with these studies. The traps were set in two lines parallel to the gap's longest axis, with an inter-trap distance of 5 m. Inside the forest, and approximately 20 m away from the edge of the gap, another 10 traps were set. Five gaps and five corresponding non-gaps were trapped at a time.

In the logged forest, 10 forest patches ranging in size from 550 m^2 to 2709 m^2 were selected. The design was similar to that in the mature forest, except that the 20 m distance was measured from the edge of a forest patch into the gap, and the understory samples were taken from the center of the forest patches.

Monthly trapping was conducted for three consecutive nights and two days at each station between March and June 1993. Therefore, a total of 600 trap-nights was achieved each month in each forest.

Traps were checked twice a day, between 0730 hours and 1300 hours, and between 1600 and 1800. Traps were emptied into plastic bags and rodents were identified to species (taxonomy followed Delany 1975), weighed, sexed, marked using standard toe and ear clipping, and subsequently released at the place of capture.

Statistical Analysis

Differences between mature and logged forests were tested using the Mann-Whitney U test (Siegel & Castellan 1988). Analyses were conducted in two ways: number of unique individuals caught per 100 traps (referred to as number of unique individuals hereafter), and trap success.

$$\text{Trap success} = 100 \times \frac{\text{catch}}{\text{No. trap-nights} - (\text{No. of sprung traps}/2)}$$

It is necessary to divide the number of traps that sprung accidentally by two because traps were inspected twice daily, and remained open for not more than a trap-night (Jeffrey 1977, Isabirye-Basuta 1979). Sample size was 20 in each forest type (i.e., 10 gap and 10 understory locations).

Kruskal-Wallis tests were used to identify differences among habitat types (i.e., gaps and understory of mature forest, and gaps and understory of logged forest) and a posteriori tests (p < 0.05) (Siegel & Castellan 1988) were used to identify differences between habitat types for all the six possible pair-wise combinations. The relationships between number of unique individuals and trap success (for each species) with gap size in the mature forest, and with forest patch size in the logged forest were tested using correlation analysis.

For each species, the relationship between two dependent variables (number of unique individuals, and trap success) and three independent variables (volume of fallen

wood, ground vegetation cover and litter depth) was examined using multiple regression analysis. Partial correlation analyses quantified the relationships between number of unique individuals and trap success, and each of the independent variables when linear effects of the other two independent variables were removed.

The relationship between the probability of *Mimusops* and *Strombosia* seeds and seedlings being present at the final census, and two independent variables, trap success, and number of unique individuals of seed eating rodents, *Praomys jacksoni* (de Winton), *Hylomyscus stella* (Waterhouse), *Hybomys univittatus* (Peters), and *Mus minutoides* (Smith) were investigated in logistic regressions. These analyses assume that trap success of these rodents was proportional to the time they foraged in the vicinity of the seed and seedlings. Correlation analyses were used to investigate the relationship between trap success and number of unique individuals and the rate of seed disappearance, and seedling mortality.

Results
Abundance and Distribution of Small Mammal Species

856 small mammals belonging to nine species were caught in the two forest compartments (mature forest- 464 individuals; logged forest- 392 individuals). Monthly trap success (for all species combined) during the four month trapping period, was higher in the mature forest (average =

65.4 ± 2.5 n = 4) than in the logged forest (average = 48.3
± 3.55 n=4) (Figure 4-1, U = 26, p = 0.014).

   Praomys jacksoni was the most common species in both
compartments, accounting for 51% (237 rodents) and 42% (167
rodents) of the total number of individuals caught in the
mature and logged forest compartments, respectively (Figure
4-2). *Hylomyscus stella* was the second most common species
in the mature forest, where it accounted for 27% (114
individuals) of the total number of individuals caught. In
the logged forest, *H. stella* ranked third in abundance and
accounted for 18% (71 individuals) of the total number of
individuals caught. *Hybomys univittatus* was the second most
abundant species caught in the logged forest, where it
accounted for 20.9% (82 individuals) of the total number of
individuals caught. It ranked third in the mature forest
and accounted for 10.3% (48 individuals) of the total number
of individuals caught in this compartment. *Lophuromys
flavopunctatus* (Thomas) and *Mus minutoides* were caught in
reasonable numbers in both compartments. *Malacomys longipes*
(Milne Edwards) (2 individuals), *Crocidura* sp (insectivora)
(3 individuals), and *Dendromys mystacalis* (Heuglin) (1
individual) were caught only rarely. *Malacomys longipes* and
Crocidura were caught in the mature forest only and *D.
mystacalis* was caught in the logged forest only. One
unidentified squirrel was caught in the logged forest.

Differences in Number of Unique Individuals and Trap success Between Forest Compartments and Among Habitat Types

Excluding rarely caught species, the number of unique individuals caught per 100 trap nights, and trap success were both higher in mature forest than in the logged forest (Tables 4-1 and 4-2). These differences were accounted for mainly by *P. jacksoni* and *H. stella*. Number of unique individuals and trap success for *H. univittatus* were higher in the logged than in the mature forest (Table 4-1), while number of unique individuals and trap success for *L. flavopunctatus* and *M. minutoides* did not differ between logged and mature forests.

The number of unique individuals differed among gaps and understories of mature and logged forests (Table 4-3). Except for *H. univittatus*, trap success also differed among the four habitat types (Table 4-4). In the mature forest, however, number of unique individuals and trap success (Tables 4-3 and 4-4) respectively, did not differ between gaps and understory at the alpha level ($p < 0.05$) whether species were combined or not. However, at the alpha-level ($p < 0.1$) number of unique individuals and trap success of *M. minutoides* were higher in gaps than understory of the mature forest. In the logged forest, both number of unique individuals and trap success of *H. stella* were higher in the understory than in gaps. In contrast to *H. stella*, the number of unique individuals and trap success of *L. flavopunctatus* were higher in gaps than the understory in the logged forest.

Relationship Between Number of Unique Individuals per 100
Trap Nights and Trap Success, and Forest Patch Size

It was predicted that the number of unique individuals
and trap success of forest rodents (e.g., *P. jacksoni* and *H.
stella*) would be positively correlated with area of the
forest patch, because these rodents prefer mature forest
(Muganga 1989). In contrast, it was predicted that number
of unique individuals and trap success of thicket-rodent
species (such as *H. univittatus*, *M. minutoides*, and *L.
flavopunctatus*) would be negatively correlated with area of
the forest patch, because these rodents are thought to
prefer thickets to mature forest (Delany 1975, Muganga
1989).

For *H. univittatus*, the number of unique individuals
and trap success of were negatively correlated with area of
forest patch (Table 4-5), suggesting that this species may
be favored by forest fragmentation. Insignificant
correlations were found for the other species, but trends
were as predicted, except for *P. jacksoni* which was
negatively related to patch size instead of positively as
predicted (Table 4-5).

Relationship Between Number of Unique Individuals per 100
Trap Nights, Trap Success and Canopy Gap Size

In the mature forest, the number of unique individuals
and trap success of forest rodents were predicted to be
negatively correlated with gap size. Number of unique

individuals and trap success of thicket rodents were
predicted to be positively correlated with gap size.

For *M. minutoides*, the number of unique individuals and
trap success were correlated positively with gap size (Table
4-6), suggesting that they may be favored by logging. The
correlation of trap success of *H. stella* with gap size was
marginally negatively correlated, suggesting this species
may not be favored by logging. Insignificant correlations
were found for the other species, but trends were as
predicted except for *P. jacksoni* which was positive instead
of negative (Table 4-6).

Correlates of Number of Unique Individuals and Trap Success

The majority of the regressions of number of unique
individuals on volume of wood, ground vegetation cover, and
litter depth (see Chapter 2 for estimation of the
independent variables) were significant (Table 4-7).
Therefore, for most rodent species, some of the variance in
number of unique individuals was explained by the
regressions. *Praomys jacksoni* (all cases), and *H.
univittatus* in the logged forest were the exception. With
the exception of *H. univittatus* (mature and logged forest
combined, and logged forest alone), and *M. minutoides* and *P.
jacksoni* in the logged forest, the rest of the regressions
of trap success on the three independent variables were
significant (Table 4-8). Thus, in most cases, some of
variances in trap success were explained by these variables.

Partial correlation analyses indicated that ground vegetation cover was in general the most important independent variable influencing number of unique individuals and trap success (Tables 4-7 and 4-8), respectively. The numbers of unique individuals of the three thicket rodents *H. univittatus*, *L. flavopunctatus* and *M. minutoides* were generally positively correlated with ground vegetation cover (not so for *H. univittatus* in the logged forest).

For the two forest-rodents, *P. jacksoni* and *H. stella*, the number of unique individuals and ground vegetation cover were generally not significantly correlated (see Table 4-7 for single exception). Except for *P. jacksoni* in the logged forest, all trends were negative.

Trap success of the three thicket species was positively correlated with ground vegetation cover, although this relationship was not significant for *H. univittatus*. Correlations of trap success of the two forest species (*H. stella* and *P jacksoni*) and ground vegetation cover were generally negative although some were not significant (Tables 4-7 and 4-8).

The volume of wood was not significantly correlated with number of unique individuals for most rodent species. A significant positive correlation between number of unique individuals and volume of wood was observed for *H. stella* only when data from mature and logged forests were combined. With a few exceptions (especially *H. stella*), volume of wood

was generally not correlated with trap success for most
rodent species(Table 4-8).

No significant correlations were found between number
of unique individuals and litter depth for any rodent
species. However, litter depth was positively correlated
with trap success of *L. flavopunctatus* in the mature forest.
Significant negative correlations between litter depth and
trap success of *P. jacksoni* were observed when data for
mature forest were analyzed separately and when data for
mature and logged forests were pooled.

Rodent Trap Success and Probability of Seed and Seedling Survival

The probability of *Mimusops* seeds being present at the
final census was weakly negatively correlated with trap
success of all seed eating rodents combined (*P. jacksoni*, *H.
stella*, *H. univittatus*, *M. minutoides*) (Table 4-9).
However, this relationship was influenced mainly by the trap
success of *P. jacksoni*. In contrast, for the seedlings of
Mimusops, the probability of being present at the final
census was not correlated with trap success of any rodent
species.

For *Strombosia* seeds, there was only one positive
correlation between the probability of seeds being present
at final census and trap success of *M. minutoides* which I
believe is likely spurious because a seed predator would not
have a positive influence on seed survival. However, a

weakly significant negative correlation was established
between probability of *Strombosia* seedlings having intact
stems at final census and the combined trap success of the
four seed and seedling eating rodent species. As with
Mimusops seeds, the significance of this relationship was
due mainly to the trap success of only *P. jacksoni*.

Correlation analyses between number of days survived
by seeds, and seedlings, and rodent trap success provided
results comparable to those from the logistic regression
(Table 4-9). However, the number of days survived by
Mimusops seeds was not correlated with trap success of any
rodent species. The number of unique individuals was less
effective than trap success in predicting duration of seed
and seedling before being preyed upon and the probability of
seeds and seedlings being present at the final census (Table
4-10).

Discussion

Rodents were more abundant in the mature forest than in
the logged forest during this study and may explain why seed
and seedling (Chapters 2 and 3) losses were not higher in
the logged forest as predicted. My findings were different
from long-term studies in Kibale (April 1977 - March 1981)
(Isabirye-Basuta & Kasenene 1987), and Muganga (1989)
(January 1987 - February 1988), that reported higher rodent
densities in disturbed forests than in mature forests.

During March - June 1993, rodent populations in Kibale were unusually high. The number of individuals per catch effort was higher than in previous studies. In 2,284 trap nights in the mature forest, 464 unique individuals were caught (0.203 unique individuals/trap night). In the logged forest, 392 unique individuals were caught in 2,311 trap nights (0.17 unique individuals/trap night). In the same forest compartments, during January 1987 - February 1988, Muganga (1989) caught 105 rodents in 6,923 trap nights (0.015 unique individuals/trap night) and 168 individuals in 7,003 trap nights (0.024 unique individuals/trap night) in mature and logged forests respectively. It should, however, be noted that Muganga (1989) trapped rodents on and above the ground but I was unable to determine how many individuals he caught on the ground. Because I trapped only on the ground in this study, comparisons with Muganga's results should have included terrestrial rodents only. Hence, number of unique individuals/trap night during Muganga's study, for terrestrial rodents should be lower than reported here. Isabirye-Basuta & Kasenene's (1987) long-term study of rodents (April 1977 - March 1981) revealed two-to four-fold differences in rodent population between peak and low years in mature and logged forests, respectively. Nonetheless, monthly trap success during their study never exceeded 10%. In this study, monthly trap success ranged between 47% and 53% in the logged forest and between 62% and 68% in the mature forest (Figure 4-1).

The greater number of rodents caught in the mature forest than logged forest may have been due to an abundance of fruiting trees in the mature forest prior to this 4-month trapping period. For example, *Strombosia* fruited in this forest from May through September 1992, and *Mimusops* fruited from November 1992 through January 1993. In the logged forest, no *Strombosia* fruited and the *Mimusops* crop was much less abundant than in the mature forest. This conclusion is further strengthened by the fact that *H. stella* and *P. jacksoni*, the most important seed eaters (Isabirye-Basuta 1979), were more abundant in the mature than logged forest. The abundance of the insectivorous *L. flavopunctatus* (Delany 1975, Isabirye-Basuta 1979) did not differ between mature and logged forests. *Hybomys univittatus* and *M. minutoides* include fair amounts of seeds and seedlings in their diets (Delany 1975, Isabirye-Basuta 1979). They were, however, not more abundant in the mature than in logged forest as would be predicted by seed abundance, possibly because they live in thickets (Delany 1975) that are more abundant in logged than in mature forests.

In a four-year study (Isabirye-Basuta & Kasenene 1987), the population of *H. stella* was consistently lower in the logged forest than in the mature forest. These observations were consistent with mine, and suggest that logging may have a negative impact on this forest-rodent (Delany 1975) through reduction of the seed resource base. However, *H. stella* is a climbing rodent (Delany 1975, Muganga 1989).

Therefore, it is also possible that loss of trees, required for climbing, may have a negative impact on this rodent. The conclusion that logging may have negative effects on seed eating rodents is further strengthened by negative correlations between trap success of *H. stella* and *P. jacksoni* with ground vegetation cover which is more prevalent in logged than in mature forests. However, between January 1987 and February 1988 *H. stella* and *P. jacksoni* both were more abundant in logged forest than in the mature forest (Muganga 1989), suggesting that populations of these species are not always higher in mature than logged forests.

Seed predation experiments conducted during 1985 (Kasenene 1987), revealed faster seed removal rates in the logged than mature forest. These observations suggest rodents were more abundant in logged forest than mature forest during that time. However, seed predation experiments conducted during 1990 (Colin Chapman unpublished data) and 1992 and this study, seed predation was generally higher in the mature than in the logged forest. By trapping rodents in the two forests, this study illustrates that rodents, particularly the most common and important seed and seedling eaters were more abundant in the mature than in the logged forest. Results from Colin Chapman's seed removal experiments suggest the rodent population pattern observed here started at least two years prior to this study.

The hypothesis that rodents use gaps more frequently than the understory, on which most studies comparing seed/seedling survival between gaps and understory are based (e.g., Webb & Willson 1985, Sork 1987, Schupp 1988 a, b, Schupp & Frost 1989, Myster & McCarthy 1989, Turner 1990, Forget 1991, Chapters 2 & 3, this study), was not supported by my study for the abundant rodent species *P. jacksoni* and *H. stella*. Trap success of *P. jacksoni*, a seed/seedling predator, was not different between gaps and understory in the mature or in the logged forest. *Hylomyscus stella* was caught even more frequently in the understory than in gaps in the logged forest. In the mature forest, trap success of *H. stella* was not different between gaps and understory. The negative correlation between *H. stella* trap success and gap size suggest that the species is not favored by extensive gaps. The only species whose trap success was consistent with the hypothesis, at least in the logged forest, was the insectivorous *L. flavopunctatus* (Delany 1975, Muganga 1989). In summary, predictions of seed and seedling predation between gaps and understory should consider a wider range of habitat variables such as, other classes of seed predators and habitat characteristics that might influence foraging efficiency of seed and seedling predators in addition to rodent populations.

Conclusions

1) Comparing the results obtained from my study of rodent abundance with those from other rodent studies in Kibale indicates that rodent populations may fluctuate widely. Furthermore, it is not always true that rodent population densities are higher in logged than in mature forests.

2) Some significant negative correlations between trap success of *H. stella* and *P. jacksoni* and ground vegetation cover were established. These observations suggest that processes that encourage growth of ground vegetation cover, such as logging, may have negative effects on the most common forest seed-eating rodent species.

3) None of the abundant seed and seedling eating rodent species was caught more frequently in gaps than in the understory. However, some significant differences in seed predation between gaps and understory were established. Therefore, more environmental parameters, such as density of alternative foods and predation pressure on rodents themselves need to be incorporated in predictions of seed and seedling predation between gaps and understory.

Table 4-1: Number of unique individuals caught per 100 trap
nights in mature forest (K30) and logged forest (K15).
Differences were tested with the Mann-Whitney U test, The
sample consisted of 10 gaps and 10 understory locations, in
each forest.

Species	Mature forest	Logged forest	Z	p
All species				
Average	24.38	18.92	-3.80	=0.0001
S.D.	3.54	3.87		
P. jacksoni				
Average	12.78	8.38	-4.38	<0.0001
S.D.	3.49	1.59		
H. stella				
Average	5.77	3.20	-2.96	=0.003
S.D	2.33	2.1		
H. univittatus				
Average	2.36	3.85	-2.22	=0.0264
S. D.	1.48	1.96		
L. flavopunctatus				
Average	1.57	1.64	-0.38	=0.6991
S.D.	1.59	2.22		
M. minutoides				
Average	1.40	1.69	-0.55	=0.5832
S.D.	1.56	1.77		

Table 4-2: Average trap success in mature forest (K30) and logged forest (K15). Differences were tested with the Mann-Whitney U test, the sample consisted of 10 gaps and 10 understory locations in each forest type. Number of trap-nights was 120 at each location.

Species	Mature forest	Logged forest	Z	p
All species				
Average	63.00	47.30	-4.50	<0.0001
S.D.	6.32	9.8		
P. jacksoni				
Average	35.53	21.21	-4.71	<0.0001
S. D.	10.10	5.19		
H. stella				
Average	12.85	7.76	-2.57	=0.0102
S. D.	5.33	6.88		
H. univittatus				
Average	8.44	10.78	-1.14	=0.2558
S.D.	6.01	7.03		
L. flavopunctatus				
Average	3.57	5.01	-0.43	=0.9657
S.D.	5.04	6.84		
M. minutoides				
Average	2.14	2.68	-0.42	=0.6707
S.D.	2.46	2.91		

Table 4-3: Number of unique individuals per 100 trap nights in gaps and understory mature forest (K30) and gaps and understory of logged forest (K15). Differences were tested with the Kruskal-Wallis test, sample size for each habitat type was 10. Row averages with the same letter were not separated by a posteriori test (p < 0.05).

Habitat type

Species	Mature forest gap	Mature forest under story	Logged forest gap	Logged forest under story	x^2	p
All species						
Average	26.34[b]	22.42[ab]	20.26[a]	17.58[a]	19.70	=0.0002
S. D.	3.40	2.53	3.87	3.80		
P. jacksoni						
Average	12.33[b]	13.23[b]	8.22[a]	8.54[a]	19.47	=0.0002
S.D	3.36	3.73	1.78	1.46		
H. stella						
Average	6.04[b]	5.52[b]	1.91[a]	4.65[b]	16.11	=0.0011
S.D	2.51	2.24	1.28	1.88		
H. univittatus						
Average	3.33[ab]	1.93[a]	4.16[b]	3.54[ab]	8.11	=0.0438
S.D.	1.66	0.90	1.82	2.16		
L. flavopunctatus						
Average	2.19[b]	0.96[ab]	3.29[b]	0.00[a]	17.78	=0.0005
S.D.	1.7	1.26	2.09			
M. minutoides						
Average	2.20[ab]	0.61[a]	2.60[b]	0.77[ab]	12.00	=0.0074
S.D.	1.75	0.83	1.97	0.94		

Table 4-4: Average trap success in gaps and understory of mature forest (K30) and gaps and understory of logged forest (K15). Differences were tested with the Kruskal-Wallis test, sample size for each habitat type was 10. Each sample (location) contained 120 trap-nights. Row averages with the same letter were not separated by a posteriori test (p < 0.05).

Habitat type

Species	Mature forest gap	Mature forest under story	Logged forest gap	Logged forest under story	x^2	p
All species						
Average	64.41[b]	61.59[b]	48.32[a]	46.28[a]	21.12	=0.0001
S.D.	5.24	7.23	9.9	10.06		
P. jacksoni						
Average	31.42[bc]	39.64[c]	20.38[a]	22.03[ab]	23.94	<0.0001
S.D	8.13	10.50	4.07	6.23		
H. stella						
Average	13.24[b]	12.46[b]	3.15[a]	12.37[b]	16.85	=0.0008
S.D.	5.47	5.45	3.19	6.52		
H. univittatus						
Average	10.38[a]	6.50[a]	11.47[a]	10.09[a]	3.54	=0.315
S.D.	5.53	6.10	6.17	8.08		
L. flavopunctatus						
Average	5.78[ab]	1.36[a]	10.01[b]	0.00[a]	19.91	=0.0002
S.D.	6.26	1.89	6.57	0.00		
M. minutoides						
Average	3.42[ab]	0.85[a]	4.00[b]	0.93[a]	12.77	=0.0052
S.D.	3.21	1.06	3.33	1.22		

Table 4-5: Correlations between number of unique
individuals per 100 trap nights, and trap success and area
of remnant forest patches in the logged forest K15. One
hundred and twenty traps were set in each of 10 forest
patches between March and June 1993 inclusive.

Species		r	p	df
H. stella	Unique individuals	+0.122	=0.7360	8
	Trap success	+0.221	=0.536	8
H. univittatus	Unique individuals	-0.848	=0.0019	8
	Trap success	-0.716	=0.0202	8
L. flavopunctatus*	Unique individuals			
	Trap success			
M. minutoides	Unique individuals	-0.244	=0.4967	8
	Trap success	-0.290	=0.4165	8
P. jacksoni	Unique individuals	-0.061	=0.8680	8
	Trap success	-0.345	=0.3288	8

* species not caught in forest patches.

Table 4-6: Correlations between number of unique
individuals per 100 trap nights, and trap success and area
of canopy gaps in the mature forest K30. One hundred and
twenty traps were set in each of 10 gaps between March and
June 1993 inclusive.

Species		r	p	df
H. stella	Unique individuals	-0.532	=0.1135	8
	Trap success	-0.694	=0.059	8
H. univittatus	Unique individuals	+0.159	=0.6614	8
	Trap success	+0.448	=0.193	8
L. flavopunctatus	Unique individuals	+0.400	=0.254	8
	Trap success	+0.025	=0.946	8
M. minutoides	Unique individuals	+0.784	=0.0073	8
	Trap success	+0.888	=0.0006	8
P. jacksoni	Unique individuals	+0.158	=0.662	8
	Trap success	+0.074	=0.834	8

Table 4-7: Regression analyses of number of unique individuals per 100 trap nights (five most common species) on volume of wood, ground vegetation cover (GVC), and litter depth. Analyses were performed for mature forest (K30) and logged forest (K15) separately, and when data from both forests were combined. Sample size was 20 in each forest (i,e,. 10 gaps and 10 understory locations).

Species	Forest type	Multiple regressions		Partial correlations		
		R	p	Wood	GVC	Litter
Hs	Mature + Logged	0.663	=0.0001	$+0.415^{**}$	-0.468^{**}	$+0.147^{ns}$
	Mature alone	0.652	=0.0277	$+0.248^{ns}$	-0.407^{ns}	$+0.335^{ns}$
	Logged alone	0.663	=0.0232	$+0.315^{ns}$	-0.383^{ns}	$+0.306^{ns}$
Hu	Mature + Logged	0.413	=0.0781	$+0.044^{ns}$	$+0.384^{*}$	$+0.265^{ns}$
	Mature alone	0.674	=0.0188	$+0.187^{ns}$	$+0.631^{**}$	$+0.385^{ns}$
	Logged alone	0.170	=0.9220	$+0.056^{ns}$	$+0.166^{ns}$	$+0.091^{ns}$
Lf	Mature + Logged	0.769	<0.0001	$+0.144^{ns}$	$+0.768^{***}$	$+0.234^{ns}$
	Mature alone	0.786	=0.0012	-0.007^{ns}	$+0.783^{***}$	$+0.427^{ns}$
	Logged alone	0.788	=0.0012	$+0.076^{ns}$	$+0.755^{***}$	$+0.207^{ns}$
Mm	Mature + Logged	0.626	=0.0004	$+0.155^{ns}$	$+0.602^{***}$	-0.083^{ns}
	Mature alone	0.739	=0.0047	$+0.260^{ns}$	$+0.699^{***}$	-0.221^{ns}
	Logged alone	0.558	=0.1049	$+0.151^{ns}$	$+0.524^{*}$	$+0.018^{ns}$
Pj	Mature + Logged	0.296	=0.342	$+0.122^{ns}$	-0.191^{ns}	-0.246^{ns}
	Mature alone	0.396	=0.422	$+0.023^{ns}$	-0.157^{ns}	-0.362^{ns}
	Logged alone	0.383	=0.454	-0.030^{ns}	$+0.058^{ns}$	$+0.371^{ns}$

Hs = *H. stella*, Hu = *H. univittatus*, Lf = *L. flavopunctatus*, Mm = *M. minutoides*, Pj = *P. jacksoni*.

ns: p > 0.05
* : p < 0.05
**: p < 0.01
***:p < 0.001

Table 4-8: Regression analyses of trap success (five most common species) on volume of wood, ground vegetation cover (GVC), and litter depth. Analyses were performed for mature forest (K30) and logged forest (K15) separately, and when data from both forests were combined. Sample size was 20 in each forest (i.e., 10 gaps and 10 understory locations).

Species	Forest types	Multiple regressions		Partial correlations		Litter
		R	p	Wood	GVC	
Hs	Mature + Logged	0.703	<0.0001	$+0.477^{**}$	-0.546^{***}	-0.016^{ns}
	Mature alone	0.614	=0.0503	$+0.405^{ns}$	-0.407^{ns}	$+0.076^{ns}$
	Logged alone	0.758	=0.0028	$+0.578^{*}$	-0.461^{*}	$+0.166^{ns}$
Hu	Mature + Logged	0.302	=0.3230	$+0.263^{ns}$	$+0.186^{ns}$	$+0.055^{ns}$
	Mature alone	0.575	=0.0853	$+0.527^{*}$	$+0.266^{ns}$	-0.039^{ns}
	Logged alone	0.037	=0.9993	$+0.026^{ns}$	$+0.014^{ns}$	-0.015^{ns}
Lf	Mature + Logged	0.680	<0.0001	-0.031^{ns}	$+0.671^{***}$	$+0.284^{ns}$
	Mature alone	0.812	=0.0005	-0.381^{ns}	$+0.758^{***}$	$+0.789^{***}$
	Logged alone	0.692	=0.0132	-0.053^{ns}	$+0.614^{**}$	-0.012^{ns}
Mm	Mature + Logged	0.584	=0.0016	$+0.166^{ns}$	$+0.564^{***}$	-0.060^{ns}
	Mature alone	0.660	=0.0243	$+0.278^{ns}$	$+0.616^{**}$	-0.161^{ns}
	Logged alone	0.536	=0.1344	$+0.008^{ns}$	$+0.471^{*}$	-0.001^{ns}
Pj	Mature + Logged	0.431	=0.0574	$+0.037^{ns}$	-0.347^{*}	-0.356^{*}
	Mature alone	0.689	=0.0141	-0.047^{ns}	-0.506^{*}	-0.602^{**}
	Logged alone	0.389	=0.4388	$+0.296^{ns}$	-0.086^{ns}	-0.086^{ns}

Hs = *H. stella*, Hu = *H. univittatus*, Lf = *L. flavopunctatus*, Mm = *M. minutoides*, Pj = *P. jacksoni*.

ns: p > 0.05
* : p < 0.05
** : p < 0.01
***:p < 0.001

Table 4-9 Logistic regression analyses of rodent trap
success and the probability of seeds and seedlings of
Mimusops and *Strombosia* being alive at final census. And
correlations of trap success and number of days survived by
Mimusops and *Strombosia* seeds and seedlings. Mature and
logged forest samples were pooled in these analyses.

Plant item	Rodent species	Logistic regressions		Correlations	
		R	p	r	p
Mimusops					
seeds	Pj+Hs+Hu+Mm	-0.127	0.104	-0.002	0.992
	Pj	-0.131	0.101	-0.015	0.927
	Hs	0.000	0.954	-0.144	0.393
	Hu	0.000	0.615	-0.121	0.477
	Mm	0.000	0.204	-0.093	0.585
Mimusops					
seedlings	Pj+Hs+Hu+Mm	0.000	0.764	-0.115	0.500
	Pj	0.000	0.648	-0.117	0.489
	Hs	0.000	0.583	-0.050	0.768
	Hu	0.000	0.987	-0.055	0.746
	Mm	0.000	0.385	-0.017	0.918
Strombosia					
seeds	Pj+Hs+Hu+Mm	0.000	0.955	-0.031	0.857
	Pj	0.000	0.873	+0.034	0.841
	Hs	0.000	0.441	-0.173	0.304
	Hu	0.000	0.866	-0.092	0.589
	Mm	+0.130	0.097	+0.269	0.107
Strombosia					
seedlings	Pj+Hs+Hu+Mm	-0.185	0.066	-0.287	0.085
	Pj	-0.262	0.029	-0.316	0.056
	Hs	0.000	0.504	-0.068	0.687
	Hu	0.000	0.426	+0.054	0.748
	Mm	0.000	0.663	+0.047	0.782

Pj = *Praomys jacksoni*, Hs = *Hylomyscus stella*, Hu = *Hybomys
univittatus*, Mm = *Mus minutoides*.

Table 4-10: Logistic regression analyses of number of
unique individuals and the probability of seeds and
seedlings of *Mimusops* and *Strombosia* being alive at final
census. And correlations of number of unique individuals
and number of days survived by *Mimusops* and *Strombosia* seeds
and seedlings. Mature and logged forest samples were pooled
in these analyses.

Plant item	Rodent species	Logistic regressions		Correlations	
		R	p	r	p
Mimusops seeds	Pj+Hs+Hu+Mm	-0.176	0.072	-0.051	0.760
	Pj	-0.217	0.049	-0.109	0.520
	Hs	0.000	0.905	+0.108	0.526
	Hu	0.000	0.376	+0.076	0.656
	Mm	0.000	0.301	-0.190	0.260
Mimusops seedlings	Pj+Hs+Hu+Mm	0.000	0.372	+0.102	0.548
	Pj	0.000	0.821	-0.034	0.842
	Hs	0.000	0.183	-0.140	0.408
	Hu	0.000	0.344	-0.039	0.818
	Mm	0.000	0.727	-0.148	0.379
Strombosia seeds	Pj+Hs+Hu+Mm	0.000	0.785	-0.037	0.827
	Pj	0.000	0.552	-0.003	0.986
	Hs	0.000	0.293	-0.124	0.465
	Hu	0.000	0.793	-0.187	0.267
	Mm	+0.160	0.075	+0.302	0.069
Strombosia seedlings	Pj+Hs+Hu+Mm	0.000	0.173	-0.206	0.221
	Pj	0.000	0.167	-0.203	0.226
	Hs	0.000	0.181	-0.217	0.198
	Hu	0.000	0.517	-0.098	0.598
	Mm	0.000	0.732	-0.084	0.619

Pj = *Praomys jacksoni*, Hs = *Hylomyscus stella*, Hu = *Hybomys
univittatus*, Mm = *Mus minutoides*.
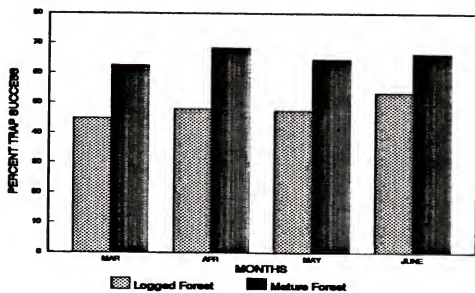
Figure 4-1: Monthly rodent trap success in mature and logged compartments of Kibale Forest between March and June 1993 inclusive.
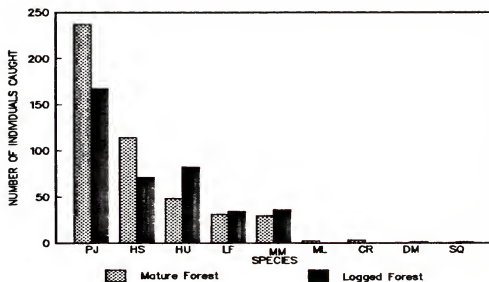
Figure 4-2: Small mammal species and number of individuals caught in a mature forest (K30) and logged forest (K15) of Kibale Forest between March and June 1993. PJ = *Praomys jacksoni*, HS = *Hylomyscus stella*, HU = *Hybomys univittatus*, LF = *Lophuromys flavopunctutas*, MM, *Mus minutoides*, ML = *Malacomys longipes*, CR = *Crocidura* species, DM = *Dendromys mystacalis*, SQ = Squirrel.

CHAPTER 5

IS REGENERATION OF *MIMUSOPS BAGSHAWEI* AND *STROMBOSIA SCHEFFLERI* IN LOGGED FORESTS HINDERED BY ELEPHANTS?

Introduction

Elephants have been reported to change the structure and composition of vegetation in several African ecosystems (Buechner & Dawkins 1961, Lamprey et al. 1967, Laws 1970, Vesy-Fitzgerald 1973, Anderson & Walker 1974, Laws et al. 1975, Leuthold 1977, Eltringham 1980, Cumming 1982, Kortlandt 1985, Mmalyosi 1987, Ruess and Halter 1990). Populations of some tree species are negatively affected by browsing (Jackmann 1989, Kalemera 1989, Ruess & Halter 1990). In Kibale Forest, Uganda (Kasenene 1984, 1987, Nummelin 1990), as well as in other African tropical rain forests (Short 1983, Merz 1986, Prins & Reitsma 1989, Barnes et al. 1991), elephants browse more frequently in secondary than in mature forests. Elephant browsing includes snapping, bending, uprooting, and pushing-over juvenile trees (Wing & Buss 1970, Kasenene 1980, 1987). Through their destructive feeding, elephants can retard the regeneration of some tree species in secondary forests (Kasenene 1984) and could determine the composition and structure of the regenerating forest. Although deformed adult trees of timber species were left by loggers to provide seeds for regenerating logged areas in Kibale, the regeneration of most trees is unsatisfactory.

Mimusops and *Strombosia* are among the common tree species browsed by elephants in Kibale (Wing & Buss 1970 Kasenene 1980, 1984, 1987). Elephants browse on *Mimusops* and *Strombosia* more than expected by chance Wing & Buss (1970). Casual observations during this study also indicated that elephants browsed selectively on saplings and poles of *Mimusops* and *Strombosia*. It was not uncommon to find freshly browsed *Mimusops* and *Strombosia* trees whenever elephants came through an area of the forest. When browsing on trees, elephants usually broke, bent, or pushed trees over.

Based on the reported selection of *Mimusops* and *Strombosia* (Wing & Buss 1970), on observations of elephant foraging, and because elephants in Kibale forage more in logged forests than in mature forests, (Kasenene 1987, Nummelin 1990), one would expect that regeneration of *Mimusops* and *Strombosia* in logged forests might be retarded through elephant foraging. Thus, the proportion of damaged *Mimusops* and *Strombosia* trees (i.e., snapped, bent or pushed-over) and multiple breaks would be expected to be higher in logged forests than in mature forests.

Here, I examine whether the slow regeneration of *Mimusops* and *Strombosia* in the logged forest (K15), and in the logged-and-treated forest (K13), could be a function of browsing of saplings and poles by elephants in these forests. Elephant browsing on *Mimusops* and *Strombosia* saplings and poles is compared among the logged forest,

logged-and-treated forest, and the mature forest (K30). The
mature forest is used as the control in these comparisons.

Methods and Materials

Selection Ratios

Elephants visited the logged forest and the mature
forest in March and April of 1993. Nineteen 5 m x 20 m
plots were established along elephant paths in each of the
forest compartments. Intersections of the regular trails
and elephant paths were used as starting points for the
sample plots. All stems of woody species $\geq$ 2.5 cm and < 14
cm diameter at breast height (dbh) that were within 2.5 m of
the center of the elephant path were measured (dbh),
identified to species (following Hamilton 1981 and Berg &
Hijman 1989), and inspected for elephant damage.
Unidentifiable species were given identification numbers or
recorded by their local names. Small individuals (< 2.5 cm
and $\geq$ 1 cm diameter) of woody species were sampled along
strips of 1 m on either side of the center of elephant
paths. Selection ratios were calculated as the proportion
of each species damaged by elephants divided by the
proportion of the species in the sampled area (Crawley
1983).

Quantification of Elephant Damage

Old damage on *Mimusops bagshawei*, and *Strombosia
scheffleri* trees $\geq$ 2.5 cm dbh was sampled along line

transects in the mature forest, logged forest, and logged-and-treated forest. Stem condition was classified according to the following criteria: intact (not damaged), snapped (if snapped, number of visible breaks was recorded), and bent. Transects followed established north-south trails in the logged, and logged-and-treated forests, and they were 100 m apart. In the mature forest, transects were 100 m apart and followed northeast-southwest trails. Transect width was 2.5 m on either side of the center of the trail. Transect length was 8,700 m (4.35 ha) in the mature forest, 10,650 m (5.33 ha) in the logged forest, and 5,250 m (2.63 ha) in logged-and-treated forest. For analysis transects were subdivided into plots 50 m long (250 m^2).

In the mature forest, *Mimusops* and *Strombosia* are generally found on mid and lower slopes. The mature forest appeared to be steeper than the logged, and logged-and-treated forests. Therefore, slope was measured and compared among forest types. The relationship between slope and stem density of *Mimusops* and *Strombosia* was investigated in the mature forest where densities were not affected by logging. Slope was measured with a clinometer at the start, center, and end of each plot, and average slope for the plot is reported.

Statistical Analysis

Differences in *Mimusops* and *Strombosia* stem density among compartments were tested with the Mann-Whitney U test

(Siegel & Castellan 1988) for all three possible pair-wise combinations. Each plot was a sample unit in this analysis. Differences in proportions of stems that were damaged among compartments were tested using the 2 X 2 contingency G - test (Sokal & Rohlf 1969) for all three possible pair combinations. Analysis was done on the actual number of stems. The influence of slope on stem density was investigated using correlation analysis.

<div align="center">Results</div>

Selection Ratios

Out of 602 woody stems (dbh $\geq$ 1 cm and $\leq$ 14 cm) belonging to 55 species that were encountered along elephant paths, 152 (25.2%) stems were damaged by elephants (Table 5-1). Elephant damage was observed on 25 plant species. Fifteen species were selectively damaged by elephants i.e., selection ratios > 1, (Crawley 1983).

Mimusops and *Strombosia* were the eighth and tenth most frequently selected species, respectively (Table 5-1). These findings suggest that elephants may have a negative impact on the regeneration of these tree species particularly in secondary forests they visit frequently.

Snapping was the most common type of damage (86%); other types of damage (14%) were less common. Hereafter, all three types are collectively referred to as browsing. Although sampling did not segregate damaged-and-browsed, from damaged-not browsed trees, the terms damage and browse

are used synonymously, because from my field experience I
know that elephants consume parts of all plants with
selection ratios of ≥ 1 (Table 5-1). Furthermore, all
species that were selected by elephants in this study were
recorded as elephant food species (Wing & Buss 1970). With
the exception of *Ficus asperifolia* (*urceolaris*) and
Chrysophyllum gorungosanum, all species selected by
elephants in this study (Table 5-1), were also selectively
browsed in a study by Wing & Buss (1970). Because plants
damaged by elephants in this study are important in the
elephant diet, the term selection ratio is appropriate here.

Size Class Distribution of *Mimusops* and *Strombosia* in Mature and Logged Forest Compartments

Mimusops: Size class distribution of forest trees
often follows an inverse exponential curve (Richards 1966).
The size class distribution of *Mimusops* trees in the mature
forest approximated an inverse exponential curve (Figure 5-
1), suggesting that it was regenerating normally in this
part of the forest. In the heavily logged forest, and the
heavily logged-and-treated forest, size class distribution
of *Mimusops* did not conform with the inverse exponential
curve. Only one individual of *Mimusops* (dbh about 10 cm)
was encountered in the logged-and-treated. Smaller
individuals were encountered in the logged forest, but
densities were low (Figure 5-1). These observations suggest
that regeneration of *Mimusops* in the disturbed forests was

impaired. Density of *Mimusops* trees < 10 cm dbh was
significantly higher in the mature forest than in the logged
forest and in the heavily logged-and-treated forest (Table
5-2). Similarly, density of *Mimusops* trees ≥ 10 cm dbh was
higher in the mature forest than in the logged, and logged-
and-treated forests (Table 5-3). Stem density of *Mimusops*
(both size classes) did not differ significantly between the
two disturbed forests (Tables 5-2 and 5-3).

   Strombosia: Size class distribution of *Strombosia*
trees approximated the inverse exponential curve in all
three forest compartments considered (Figure 5-2). The
apparent high density of trees > 10 cm dbh, especially in
the mature forest is the result of using a lager size class
interval (10 cm interval) in the latter part of the graph.
Density of *Strombosia* stems < 10 cm dbh was marginally
higher in the mature forest than in the logged forest (Table
5-2). The difference in stem density of *Strombosia* (dbh <
10 cm) between mature forest, and logged-and-treated forest
was not significant. Stem density of *Strombosia* (< 10 cm
dbh) was higher in the logged-and-treated forests than
logged forest(Table 5-2). For the larger size class (dbh ≥
10 cm dbh), *Strombosia* stem density was significantly higher
in the mature forest than in the logged and logged-and-
treated forests (Table 5-3), but the two disturbed forests
did not differ in stem density (dbh ≥ 10 cm).

Differences in *Mimusops* and *Strombosia* Stem Damage Among Forest Compartments

Two types of stem damage, snapping and bending, were recorded. The majority of damages were snaps (see below). Stems with multiple snaps were recorded as a subcategory of snapped stems. Statistical analysis was conducted on damaged stems (snapped at least once + bent stems) (Table 5-4) and on stems with multiple breaks (Table 5-5).

Mimusops : In the mature forest, 54 *Mimusops* stems (dbh < 10) were recorded; of these, 16 (30%) were snapped. In the heavily logged forest, nine stems (dbh < 10) were encountered, eight (89%) of these were damaged (snapped = 6, bent = 2). The proportion of *Mimusops* stems that were damaged was higher in the logged forest than in the mature forest (Table 5-4). Only one bent stem of *Mimusops* (dbh < 10) was encountered in the heavily logged-and-treated forest; thus stem damage was not compared between the logged-and-treated forest and the other forest compartments.

For the large size class (dbh $\geq$ 10 cm), 13 stems were encountered in the mature forest, none of them was damaged. One bent *Mimusops* stem (dbh $\geq$ 10) was encountered in the logged forest.

Multiple breaks were observed on stems (dbh < 10 cm). Of the 16 *Mimusops* stems (dbh < 10 cm) that were damaged in the mature forest, only two (12.5%) were snapped more than once. In the logged forest, four (50%) out of eight damaged stems were snapped more than once. However, the number of

stems snapped more than once did not differ significantly between the two compartments (Table 5-5).

Strombosia: Out of the 86 *Strombosia* stems (dbh < 10 cm) recorded in the mature forest, 11 (12.8%) were damaged (bent = 1, snapped = 10). In the logged forest, out of 73 stems encountered, 40 (54.8%) were damaged (bent = 3, snapped = 30). The proportion of damaged stems was significantly higher in the logged forest than in the mature forest (Table 5 - 4). In the logged-and-treated forest, 36 (69%) (bent = 2, snapped = 34) out of 52 stems were damaged. The proportion of stems that were damaged was significantly higher in the logged-and-treated forest than in the mature forest. There was no difference in proportion of stems that were damaged (dbh < 10 cm) between the two disturbed forests (Table 5-4).

For the large size class (dbh $\geq$ 10 cm), none of the 71 stems encountered in the mature forest were damaged. In the logged forest, four (20%) out of 20 stems encountered were snapped. These differences were significant. The proportion of snapped stems was higher in the logged forest than in the mature forest (Table 5-4). In the logged-and-treated forest, 21 stems were encountered; and of these, three (14.2%) were snapped. When compared with the mature forest, a significantly higher proportion of stems was snapped in the logged-and-treated forest than in the mature forest. The difference between the two disturbed forests was not significant.

Trees with multiple breaks were all < 10 cm dbh. None of the 86 *Strombosia* stems encountered in the mature forest was snapped more than once. In the logged forest, 12 (30%) of the 40 stems that were damaged had multiple breaks. Multiple breaks were significantly more common in the logged forest than in the mature forest (Table 5-5). In the logged-and-treated forest, nine (22.5%) of the 40 *Strombosia* stems that were damaged had multiple breaks. The proportion of stems with multiple breaks did not differ between the logged-and-treated forest and the mature forest. Similarly, there was no difference in proportion of *Strombosia* stems that were snapped more than once between the two disturbed forests (Table 5-5).

Does Slope Influence Stem Density of *Mimusops* and *Strombosia*?

Average slope was $13.37^O \pm 8.34^O$(S.D), $8.09^O \pm 5.9^O$(S.D), and $7.74^O \pm 5.3^O$ (S.D) in the mature forest (K30), heavily logged forest (K15), and in the heavily logged and treated forest (K13), respectively, $(F_{2, 509} = 37.69, p < 0.0001)$. Significant differences were observed between the mature forest and logged forest, and between the former and the logged-and-treated forest. Differences between the two disturbed forests were not significant (Scheffe's procedure $p < 0.05$).

The influence of slope on stem density was investigated in the mature forest only, because natural tree densities were unaffected by logging. Densities of *Mimusops* stems (<

10 cm dbh) (r = +0.194, p = 0.0065, df = 192) and those (≥ 10 dbh) (r = +0.225, p = 0.0016, df = 192) were both positively correlated with slope. For *Strombosia*, there was no correlation between density of stems < 10 cm dbh and slope (r = +0.033, p = 0.645, df = 192), however, density of stems ≥ 10 cm dbh was positively correlated with slope (r = +0.278, p = 0.0001, df = 192). Although tree distribution is also influenced by factors other than slope (as indicated by the small r-values), these observations suggest that slope contributes to the variation in density of *Mimusops* and *Strombosia* (dbh ≥ 10 cm) in the forest, and may contribute to differences in stem density (Figures 5-1 and 5-2), between mature forest and the two disturbed forests.

Discussion

Elephant damage on *Mimusops* and *Strombosia* trees < 10 cm dbh was more common in the heavily logged forest and heavily logged-and-treated forest than in the mature forest. Furthermore, *Strombosia* trees that were broken repeatedly were more common in logged forest than in the mature forest. These results suggest that elephants have a negative impact on the regeneration of *Mimusops* and, especially, *Strombosia* in logged areas.

Although stem snapping can be caused by agents other than elephants, I assumed that the majority of snapped stems in forests disturbed by logging were caused by elephants. This assumption is reinforced with data on selection of

Mimusops and *Strombosia* by elephants. It is also emphasized that this study was conducted approximately 25 years after logging. Therefore, it is very unlikely that tree damage reported here was caused by logging because, 1) breaks that occurred 25 years ago would have healed and 2) the majority of trees encountered were small (< 10 cm dbh), and probably germinated after logging.

Although stem density of *Strombosia* trees < 10 cm dbh was higher in the mature forest than in the logged forest, this difference was only weakly significant. Furthermore, stem density of *Strombosia* < 10 cm dbh was not different between the mature forest and the logged-and-treated forest. However, the proportions of stems that were damaged by elephants in the two disturbed forests were significantly greater than in the mature forest. These results suggest that regeneration of *Strombosia* in the disturbed forests is not limited by shortage of seeds as may be expected considering the low density of adult trees, but rather regeneration may be limited by elephant browsing.

The low densities of *Mimusops* stems < 10 cm dbh in the disturbed forests as compared to the mature forest suggest that regeneration of this species in the disturbed forests is to some extent limited by shortage of seeds and/or low survival of seedlings and small saplings. However, eight out of nine stems encountered in the logged forest and the one stem found in the logged-and-treated forest were damaged

by elephants, suggesting that regeneration of this species
is further hindered by elephant browsing.

Previous studies in Kibale (e.g., Wing and Buss 1970,
Kasenene, 1980, 1987) also suggest that regeneration of tree
species in logged forest is hampered by elephants. Wing and
Buss (1970) found that throughout Kibale elephants foraged
in colonizing forests more than expected by chance.
Furthermore, nearly 98% of trees utilized by elephants were
< 10 cm dbh. Because young trees damaged by elephant are
sometimes beyond recovery, (Kasenene 1980, 1987) elephants
can impair natural regeneration of species that are
selectively browsed, such as *Mimusops* and *Strombosia*.

In Kasenene's (1980) study, *Mimusops* and *Strombosia*
were among the species selected by elephants; a higher
proportion of trees < 12.7 cm dbh was damaged in a lightly
logged forest (K14) than in the mature forest (K30). In a
very lightly logged forest (K14 A), the proportion of trees
damaged did not differ between the former and in the mature
forest (Kasenene 1980). These results suggest that the
intensity of elephant damage increases with logging
intensity.

Elephants are lured into logged forests by the
luxuriant herbaceous vegetation found in large gaps
(Kasenene 1980). Therefore, if logging operations can avoid
the creation of large gaps, the forest may be less
attractive to elephants and, thereby reduce their adverse
impact on regeneration.

Although stem density of *Mimusops* and *Strombosia* $\geq$ 10 cm dbh was higher in the mature forest than in the logged forest, these differences cannot be attributed to logging alone. Only a negligible volume of *Mimusops* (< 0.01 m^3/ha) was harvested from the logged forest, and *Strombosia* was not harvested (Skorupa 1988), but adult stem density of these species was low in this forest. Therefore, apart from logging, other factors including browsing on young trees $<$ 10 cm dbh by elephants contribute to the low occurrence of adult *Mimusops* and *Strombosia* in the logged forest (K15).

Because timber harvest data for the logged-and-treated forest were combined with two other compartments (Skorupa 1988), it was impossible to estimate the impact of logging on the adult population of *Mimusops* and *Strombosia* in the logged-and-treated forest. Nonetheless, three large (dbh $\geq$ 48 cm) *Mimusops* and 91 large *Strombosia* trees were encountered during stock mapping conducted in this part of the forest prior to logging in 1968 (Forest Department Records). Unfortunately, size of the area that was mapped was not indicated in the records. These limited data suggest that *Mimusops* in the logged-and-treated forest was rare before logging but, *Strombosia* was fairly common prior to logging. The low density of *Mimusops* in this part of the forest is probably due to some natural factors. The density of adult *Strombosia* in the logged-and-treated forest could have been reduced by logging, but elephant browsing on *Strombosia* stems $<$ 10 cm dbh was also high enough to suggest

that elephants possibly prevented recruitment of these young trees into the adult population.

Slope in the mature forest was steeper than in the two disturbed forests, and there were positive correlations between stem density (> 10 cm dbh) of *Mimusops* and *Strombosia* with slope in the mature forest. These results suggest that *Mimusops* and *Strombosia* reach higher densities on slopes. The low correlation values are not surprising, because these species are generally found on mid and lower slopes (personal observation). The flatness of the disturbed forests could also have contributed to the low density of large trees, particularly of *Mimusops*.

Summary of Main Points

1) Nearly all *Mimusops* (9 out of 10) trees < 10 cm dbh encountered in disturbed forests were damaged by elephants. Some (4 out of 10) had signs of repeated browsing. It was concluded that elephants, by destroying young trees contribute to the low density of large *Mimusops* trees in disturbed forests, although other factors such as slope, may be also be important.

2) The density of *Strombosia* stems (< 10 cm dbh) in the mature forest (K30) was slightly higher than in the logged forest (K15). However, the proportion of stems that was damaged by elephants was higher in the logged forest than in the mature forest. Because large stems of *Strombosia* were not removed from the logged forest, one would expect density

of large stems of *Strombosia* not to differ very significantly between the logged and mature forests as was observed. Apparently recruitment of *Strombosia* into the large size class in the logged forest is suppressed by elephants, hence the difference in stem density of the large size class between the two compartments.

Table 5-1: Selection ratios of elephants on woody species
enumerated along elephant paths in the mature and heavily
logged forest (5 m X 380 m in each forest). Selection
ratios were obtained by dividing proportion of each species
damaged (snapped, bent or pushed over) by elephants by the
proportion of the species in the sampled area. Values $\geq$ 1
indicate selection by elephants. Out of the 602 stems that
were enumerated, 152 were damaged by elephants.

Selection Plant species	Intact	Snapped	Bent	Pushed over	Total	% Damaged	Ratio
Lovoa swynnertonii	00	01	00	00	01	100	4.0
Newtonia buchananii	00	20	00	00	20	100	4.0
Parinari excelsa	00	01	00	00	01	100	4.0
Albizia gummifera	00	03	01	00	04	100	3.96
Pygeum africanum	00	00	00	02	02	100	3.96
Antiaris toxicaria	04	23	00	00	27	85.2	3.37
Ficus exasperata	01	05	00	00	06	83.3	3.30
Mimusops bagshawei	04	17	01	01	23	82	3.27
Bosqueia phoberos	04	09	04	00	17	76.4	3.03
Strombosia scheffleri	04	08	02	00	14	71	2.83
Symphonia globulifera	05	09	00	00	14	64.3	2.54
Blighia unijugata	07	13	00	00	20	65	2.57
Chrysophyllum gorungosanum	03	02	00	00	05	40	1.58
Ficus asperifolia	12	04	04	00	20	40	1.58
Trichilia splendida	05	02	00	00	07	28.6	1.13
Celtis africana	10	02	00	01	13	13.1	0.91
Markhamia platycalyx	07	02	00	00	09	33	0.88
Conopharyngia holstii	13	02	00	01	16	18.5	0.74
Mutabwankubebe[*]	14	01	00	02	17	17.6	0.7
Vangueria apiculata	06	01	00	00	07	14.3	0.57
Cyphomandra batacea	10	01	00	00	11	9.1	0.36
Chaetacme aristata	12	01	00	00	13	7.7	0.3
Funtumia latifolia	12	01	00	00	13	7.7	0.30
Rubiaceae	18	01	00	00	19	5.3	0.21
Teclea nobilis	47	01	01	01	50	06	0.24
Dasylepis eggelingii	19	01	00	00	20	05	0.21

The following species were encountered along elephant paths, but were
not damaged by elephants. Figures indicate number of stems enumerated.
Aningeria altissima(3), *Aphania senegalensis* (4), *Cassipourea* sp (16),
Celtis durandii (13) *Citropsis schweinfurthi* (2), *Clausena anisata* (6),
Coffea eugenioides (4), *Diospyros abyssinica* (18), *Euadenia eminens* (3),
Fagaropsis angolensis (11), *Kigeria moosa* (10), *Leptonychia mildbraedia*
(4), *Linociera johnsonii* (7), *Milletia dura* (5), *Monodora myristica* (5),
Myrianthus holsti (7), *Neoboutonia macrocalyx* (1), *Neoboutonia
macrocalyx* (1), *Olea welwitschii* (1), *Oncoba spinosa* (14), *Pancovia
turbinata* (8), *Pleiocarpa pycnantha* (2), *Premna angolensis* (2),
Pseudospondias microcarpa (4), *Psychotria* sp (18), *Randia malleifera*
(25), *Randia urcelliformis* (7), Unident (12), *Uvariopsis congensis* (14).

[*] = local name.

Table 5-2: Differences (Mann-Whitney U test) in number of
Mimusops and *Strombosia* stems (dbh ≥ 2.5 cm < 10 cm) per 250
m^2 plot among mature, logged, and logged-and-treated forest
compartments of the Kibale Forest Reserve.

Species	Forest-type	Number of stems/plot	Number of plots	Z	p
Mimusops	Logged	0.042 ± 0.202	213		
	Mature	0.278 ± 0.623	194	-5.13	< 0.0001
	Logged + treated	0.010 ± 0.098	105		
	Mature	0.278 ± 0.623	194	-4.71	< 0.0001
	Logged + treated	0.010 ± 0.098	105		
	Logged	0.042 ± 0.202	213	-1.57	= 0.1163
Strombosia	Logged	0.338 ± 0.905	213		
	Mature	0.433 ± 0.904	194	-1.834	= 0.0667
	Logged + treated	0.533 ± 0.019	105		
	Mature	0.433 ± 0.904	194	-0.877	= 0.3802
	Logged + treated	0.533 ± 0.019	105		
	Logged	0.338 ± 0.905	213	-2.466	= 0.0137

Table 5-3: Differences (Mann-Whitney U test) in number of
Mimusops and *Strombosia* stems (dbh $\geq$ 10 cm) per 250 m^2 plot
among mature, logged, and logged-and-treated forest
compartments of the Kibale Forest Reserve.

Species	Forest type	Number of stems/plot	Number of plots	Z	p
Mimusops	Logged	0.005 ± 0.069	213		
	Mature	0.067 ± 0.289	194	-3.097	=0.0020
	Logged + treated	0.000 ± 0.000	105		
	Mature	0.067 ± 0.289	194	-2.482	=0.0131
	Logged + treated	0.000 ± 0.000	105		
	Logged	0.005 ± 0.069	213	-0.702	=0.4826
Strombosia	Logged	0.094 ± 0.364	213		
	Mature	0.381 ± 0.838	194	-0.442	<0.0001
	Logged + treated	0.143 ± 0.426	105		
	Mature	0.381 ± 0.838	194	-0.493	=0.0127
	Logged + treated	0.143 ± 0.426	105		
	Logged	0.094 ± 0.364	213	-1.168	=0.2426

Table 5-4: Differences in numbers of *Mimusops* and *Strombosia* stems that were damaged (snapped, bent or pushed over) among mature, logged, and logged-and-treated forest compartments of Kibale Forest Reserve. For *Mimusops*, differences between the logged and logged-and-treated forests, and between mature and logged-and-treated forests were not tested because only one *Mimusops* tree was found in in the logged-and-treated forest. Figures in parentheses are the expected values.

Species and size class	Forest type	Number of damaged stems	Number of intact stems	X2	p	df
Mimusops (dbh<10 cm)	Mature	16 (20.6)	38 (33.4)			
	Logged	8 (3.4)	1 (5.6)	4.573	<0.05	1
Mimusops (dbh≥10 cm)	Mature	0	13			
	Logged	1	0			
Strombosia (dbh<10 cm)	Mature	11 (27.6)	75 (58.4)			
	Logged	40 (23.4)	33 (49.6)	31.15	< 0.001	1
	Mature	11 (29.3)	75 (56.7)			
	Logged + treated	36 (17.7)	16 (34.3)	44.39	< 0.001	1
	Logged	40 (44.4)	33 (28.6)			
	Logged + treated	36 (31.6)	16 (20.4)	2.11	> 0.1	1
Strombosia (dbh≥10 cm)	Mature	0 (3.1)	71 (67.9)			
	Logged	4 (0.9)	16 (19.1)	8.316	< 0.01	1
	Mature	0 (2.3)	71 (68.7)			
	Logged + treated	3 (6.7)	18 (20.3)	5.15	< 0.05	1
	Logged	4 (3.4)	16 (16.6)			
	Logged + treated	3 (3.6)	18 (17.4)	0.005	> 0.1	1

Table 5-5: Differences in number of *Mimusops* and *Strombosia* stems (dhb ≥2.5 cm < 10 cm) with multiple breaks among mature, logged, and logged-and-treated forest compartments of the Kibale Forest Reserve. Figures in parentheses are the expected values.

Species and size class	Forest type	Number of stems with ≥ 2 breaks	Number of stems with 1 break	X^2	p	df
Mimusops	Mature	2 (4.0)	14 (12)			
	Logged	4 (2.0)	4 (6)	2.16	> 0.1	1
Strombosia	Mature	0 (2.6)	11 (8.4)			
	Logged	12 (9.4)	28 (30.6)	3.59	0.1>0.05	1
	Mature	0 (2.1)	11 (8.9)			
	Logged + treated	9 (6.9)	27 (29.1)	2.48	>0.1	1
	Logged	12 (11.1)	28 (28.9)			
	Logged + treated	9 (9.9)	27 (26.1)	0.05	>0.1	1
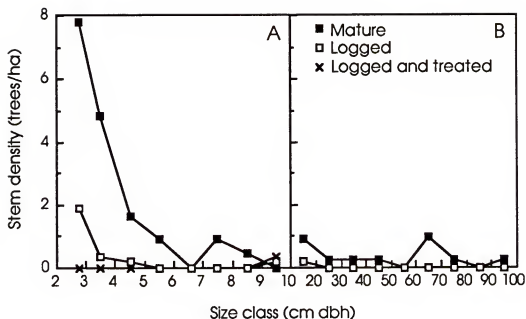
Figure 5-1: Size class (cm dbh) distribution of *Mimusops* in the mature forest (K30), heavily logged forest (K15) and heavily logged-and-treated forest (K13) of the Kibale Forest Reserve, Uganda. Diameter intervals of one-cm and 10-cm were used for trees < 10 cm dbh and > 10 cm dbh, respectively.
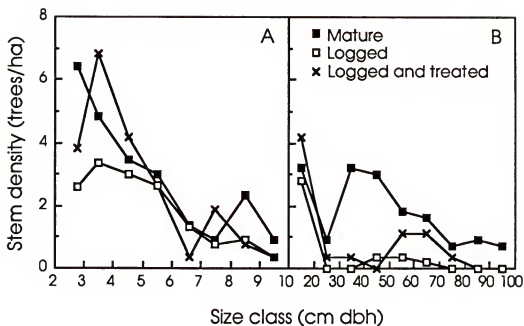
Figure 5-2: Size class (cm dbh) distribution of *Strombosia* in the mature forest (K30), heavily logged forest (K15) and heavily logged and treated forest (K13) of the Kibale Forest Reserve, Uganda. Diameter intervals of one-cm and 10-cm were used for trees < 10 cm dbh and > 10 cm dbh, respectively.

CHAPTER 6

GENERAL DISCUSSION

Survival of *Mimusops* and *Strombosia* Seeds and Seedlings in Logged and Mature Forests

Regeneration is a key issue in the conservation and management of tropical rain forests. Forestry practices that do not allow the forest to quickly regenerate will result not only in losses of forests, but also the animals that depend on forests, and the free services rendered by forests. It is therefore important to adopt management practices that ensure sustainable exploitation of forests over as a short cycle as possible. As a result, it becomes vital to understand factors that hinder regeneration of exploited forests in order to facilitate refinement of future management plans.

Selective logging is a preferred alternative to clear felling (Perry 1982, Uhl 1982, Uhl & Buschbacher 1985, Hartshorn 1989), because selective logging removes only a few trees per hectare, and, if conducted carefully, may create gaps comparable to natural tree-fall gaps. Because of the tremendous number of species that depend on natural gaps for regeneration, and thus can take advantage of gaps created by logging, selective logging has been advocated as a suitable strategy for sustained forest exploitation (Perry 1982, Uhl 1982 Uhl & Buschbacher 1985, Uhl et al. 1991. However, the fashion in which selective logging is typically

carried out is far from being sustainable, because it causes extensive damage that can in turn lead to impaired forest regeneration. For example, in the Dipterocarp forests of southeast Asia, timber harvests of about 50 m^3 per hectare leaves forests in devastated conditions (Fox 1968, 1976, Johns 1983 a, b). In Suriname, removal of only 20 m^3 per hectare caused considerable damage (Jonkers & Schmidt 1984). Similarly, in Kibale Forest, Uganda, removal of only 17 m^3 per hectare caused a 62% reduction in canopy cover (Kasenene 1987, 1988). Therefore, selective logging as it is often practiced can alter the integrity of tropical forests considerably, such as by disrupting natural plant-animal interactions, which in turn may interfere with natural regeneration.

When the canopy is extensively opened by logging, herbaceous plants respond to the increased light intensity by fast growth, and quickly form a thick tangle of vegetation which is the preferred habitat for several rodent species (Emmons 1982, Kasenene 1984, Isabirye-Basuta & Kasenene 1987, Muganga 1989, Walker & Rabinowitz 1992). Because rodents are serious predators of large forest seeds and seedlings (Janzen 1969, 1971, Sork 1987, Schupp 1988 a, b, Schupp et al. 1989), provision of suitable rodent-habitat may have a negative effect on the regeneration of logged forests. Furthermore, the luxuriant herbaceous vegetation that establishes in heavily logged forests lures elephants

that may also retard the regeneration by browsing and trampling young trees (Kasenene 1984, 1987).

In this study I examined the influence of rodent seed and seedling predation, the effect of logging, and elephant browsing on forest regeneration. Previous studies in Kibale Forest have reported higher rodent densities in the logged forests than in the mature forests, and positive correlations between ground vegetation cover and rodent densities (Isabirye-Basuta 1989, Kasenene 1984, Isabirye-Basuta & Kasenene 1987, Muganga 1989). I extended these findings to investigate differences in survival of *Mimusops* and *Strombosia* seeds, and seedlings between mature and logged forests, and between gaps and understories.

Rodents were the major causes of mortality of *Mimusops* and *Strombosia* seeds and seedlings in Kibale, suggesting that their abundance can influence forest regeneration. Hence, the influence of forest practices on rodent numbers should be given attention in forest management plans. In this study, however, seed and seedling predation was not higher in logged forests than in mature forests. Predation of *Mimusops* seeds and seedlings did not differ between mature and logged forests, while predation of *Strombosia* seed and seedlings was higher in the mature forest than in the logged forest. These unexpected results were apparently related to unusually high numbers of rodents, particularly in the mature forest(Chapter 4, Anke Hoffmann unpublished data). Contrary to the usual pattern (Isabirye-Basuta 1979,

Kasenene 1984, Isabirye-Basuta & Kasenene 1987, Muganga 1989), rodents were more abundant in the mature forest than in the logged forest. This was particularly so for *P. jacksoni* and *H. stella*, species that specialize in eating seeds and seedlings (Isabirye-Basuta 1979). The unusually high rodent populations and distribution patterns mean that the results from this study may not represent the typical patterns of seed and seedling predation in the two forest types. However, it is possible that rodent abundance in the mature and logged forests have changed because Colin Chapman (Pers. comm.) also observed higher seed predation rates in the mature forest than in the logged forest a year prior to my study.

Although seed and seedling predation were not higher in the logged forest than in the mature forest, as predicted, some of my results were consistent with what would be expected based on rodent populations during this study, (i.e., low predation was observed where rodent density was also low). Predation of *Strombosia* seeds and seedlings was lower in the logged forest where the populations of specialized seed and seedling predators were low. Losses of large seeds to forest rodents are not uncommon (Janzen 1969, 1971, Howe & Richter 1982). Long-term, seed and seedling predation of *Mimusops* and *Strombosia* may be higher in the logged forest than in the mature forest because long-term studies show that rodents are usually more abundant in logged forests than in mature forests. Although the density

of seed sources (mature trees) is lower in the logged forest than in the mature forest (Skorupa 1988, Chapter 5), the effects of seed scarcity on regeneration of logged forests may further be exacerbated by seed and seedling predation.

Rodent trap success and ground vegetation cover (such as that found in gaps) are positively correlated (Rood & Test 1968, Janzen 1970, Delany 1971, Synnott 1975, Emmons 1982, Kasenene 1984, Isabirye-Basuta & Kasenene 1987, Muganga 1989, Walker & Rabinowitz 1992). It is therefore frequently assumed that rodents forage more frequently in gaps than in the understory (Webb and Willson 1985, Sork 1987, Schupp 1988 a, b, Schupp and Frost 1989, Myster & McCarthy 1989, Turner 1990). In this study, there was no difference in trap success between gaps and understory of the mature forest, suggesting that rodents did not preferentially select one habitat over the other. However, the rodent numbers during my study were so high and possibly swamped this effect.

The influence of canopy gaps on seed and seedling predation is unclear and difficult to interpret. According to the escape hypothesis (Janzen 1970, Connell 1971, Howe at al. 1985), seed survival would be higher in gaps than in the understory, because seeds in gaps are unlikely to be beneath adult conspecifics where mortality is usually 100 % (Hartshorn 1978). However, Schupp (1988 a) contends that the dense ground vegetation cover in gaps provides refuge for rodents; hence seed predation can be higher in gaps

than in the understory. Some studies, reported higher seed
survival in gaps than in the understory (Webb & Willson 1985
Turner 1990). Schupp (1988 a) and Schupp & Frost (1989)
reported higher seed survival in the understory than in
gaps. For some seed species, Webb & Willson (1985) found no
difference between seed survival in gaps and in the
understory. In my study, significant differences in seed
and seedling survival between gaps and understory were
observed in the logged forest, but not in the mature forest.
Gaps and understories of the two forest types differed in
several characteristics, such as rodent populations, litter
depth, and ground vegetation cover. Therefore, seed and
seedling survival does not only depend on being in gaps or
in the understory, but also on the forest type in which
these habitat types are located.

In Kibale, the major seed and seedling predators and
the most abundant rodents, *H. stella* and *P. jacksoni*, were
nocturnal and may not have needed ground vegetation cover
for predator protection. Correlations of trap success of *P.
jacksoni* and *H. stella* with ground vegetation cover were
both negative, suggesting that these rodents may be avoiding
areas with thick ground vegetation cover. Therefore,
Hartshorn's (1978) suggestion that seeds in gaps are more
prone to predation because rodents are likely to be in gaps
was not supported by these two species.

Considering only logged forest, there is some advantage
to dispersal of seeds in the understories of remnant forest

patches. In the second phase of the seed predation experiment, seeds of *Mimusops* and *Strombosia* that were put in the understories survived longer than those placed in gaps. However, higher survival of seeds and seedlings in the understory was not consistent with low trap success of seed predators. Trap success of *P. jacksoni* did not differ between gaps and understory. For *H. stella*, trap success was even higher in the understory than in gaps, and thus suggesting that seed and seedling predation would be higher in the understory than in gaps. But this was not the case. These results suggest that seed and seedling predation cannot be predicted from rodent abundance alone; but other ecological factors, such as abundance of alternative foods, litter depth and other seed predators: insects, francolins and guineafowls should also be considered.

I examined the influence of ground vegetation cover, litter depth, and volume of wood on seed and seedling survival and on rodent abundance. In the logged forest, probabilities of *Mimusops* and *Strombosia* seeds surviving to final census were positively correlated with litter depth, and were negatively correlated with ground vegetation cover. These results suggest that litter depth renders some protection to seeds. Probably litter rendered seeds less conspicuous to the rodents. It should also be emphasized that significant relationships were observed when leaf litter was not removed from experimental seeds. Litter depth was not significantly negatively correlated with trap

success of any of the seed eating rodent species in the logged forest, thus weakening the assertion that litter may lower the foraging activity of rodents. However, trap success of *P. jacksoni* was negatively correlated with litter depth when data from mature and logged forest were pooled, and when data from the mature forest were considered separately. These results suggest that *P. jacksoni*, a seed eating species, forages less frequently in areas with large amounts of litter and were consistent with the assertion that litter renders protection to seeds.

Ground vegetation cover, suggested to attract rodents (Schupp 1988a) and hence predispose seeds to predation, was positively correlated with trap success of diurnal species *L. flavopunctatus* and *M. minutoides* only. These species are primarily insectivorous (Isabirye-Basuta 1979) and were at low densities, thus they may have had little influence on seed survival. Additionally, trap successes of *P. jacksoni* and *H. stella* were negatively correlated with ground vegetation cover (Table 4-8). These results suggest that *P. jacksoni* and *H. stella* forage less frequently in areas with thick ground vegetation cover. Therefore, the fate of seeds and seedlings in gaps or in the understory is apparently determined by an interaction of ecological factors that may include: density of seed and seedling predators, density of alternative foods, density of predators of rodents, litter depth and others.

Lessons Learned From Rodent Exclosure Experiments

Exclusion experiments revealed that seedling establishment for *Mimusops* would be higher in the logged forest than in the mature forest if the effects of rodents were removed. In the mature forest, and particularly in the understory, seeds of *Mimusops* were vulnerable to fungal infection (Table 2-5). Apparently, the humid conditions in the understory of the mature forest rendered *Mimusops* seeds more susceptible to fungal infection, because understories of mature continuous forests are more humid than in gaps (Lovejoy et al. 1986).

Large seeded-species generally classified as shade-tolerant species (Bazzaz & Pickett 1980, Brokaw 1985), germinate in the understory where they stay as suppressed seedlings until gaps form above them (Whitmore 1978, Bazzaz & Pickett 1980, Brokaw 1985). This study has shown that *Strombosia*, a large-seeded species, establishes equally well in gaps, and in the understory when rodents are excluded. When rodents were excluded, seedling establishment was even higher in gaps than in the understory for *Mimusops*.

Apart from establishment in gaps, the fastest growth in height of *Strombosia* seedlings were observed in the large gaps of the logged forest. These results suggest that physical environmental conditions do not account for low densities of seedlings of these large-seeded species in gaps.

Predation and low dispersal may contribute to the scarcity of these seedlings in gaps. Results of rodent exclosure studies suggest that rodents contribute to the paucity of seedlings of some large-seeded species in gaps. Large seeds in tropical forests, are predominantly dispersed by animals such as, birds, bats, and primates (Howe & Smallwood 1982, Estrada & Coates-Estrada 1991 Forget 1991). Therefore, lack of perching sites for birds, and lack of arboreal paths for primates, may contribute significantly to the rarity of seedlings of large-seeded species in gaps because seeds may not be dispersed there. This is particularly more likely to be the case in large gaps, such as those created through logging.

Elephants and the Regeneration of *Mimusops* and *Strombosia*

Regeneration in natural tree-fall gaps is accomplished by rapid growth of pre-existing seedlings and saplings, and by fast-growing pioneer trees, usually originating from the seed bank (Whitmore 1978, Brokaw 1985, 1987, Uhl & Buschbacher 1985, Kasenene 1987, Uhl et al. 1988). If carefully done, selective logging should emulate natural tree gaps, and therefore should encourage regeneration (Perry 1982, Uhl 1982, Uhl & Buschbacher 1985, Hartshorn 1989). But in reality, selective logging is not conducted carefully, and creates gaps far larger than natural tree-fall gaps (Fox 1968, 1976, Johns 1983 a, b, Kasenene 1987, Skorupa 1988). In Africa, elephants forage more frequently

in logged forests than in mature ones (Short 1983, Kasenene
1984, 1987, Merz 1986, Prins and Reitsma 1989, Nummelin
1990, Barnes et al. 1991). Furthermore, young trees are
browsed more than mature ones (Wing & Buss 1970, Chapter 5).
Therefore, the pre-existing saplings may be destroyed by
elephants. Hence regeneration in logged forests may remain
suppressed for a long time.

Elephants impinged on the regeneration of *Mimusops* and
Strombosia in the logged forests. However, the relative
importance of elephants may be different between the two
species. For example, the low density of *Mimusops* trees <
10 cm in the logged forest (K15), and in the logged-and-
treated forest (K13) may be due to shortage of seeds, and/or
high mortality of seeds, seedlings and small saplings. An
intensive search in logged forest revealed only 14 adult
Mimusops trees in an area of 1 Km² and none were encountered
in the logged-and-treated forest along a transect of 5,250
m, suggesting low seed sources in these areas. However,
nine of the 10 *Mimusops* trees (< 10 cm dbh) encountered in
both forests combined, were damaged by elephants. Hence, it
was concluded that elephants contribute to the slow
regeneration of *Mimusops* in logged forests.

Although the density of large *Strombosia* trees > 10 cm
dbh was lower in the logged forest and in the logged-and-
treated forest than in the mature forest, apparently
regeneration of this species in the disturbed forests was
not limited by shortage of seeds because, the density of

young *Strombosia* trees < 10 cm dbh, was only marginally higher in mature forest than in the logged forest (Table 5-2). Furthermore, stem density of *Strombosia* trees < 10 cm dbh did not differ between logged-and-treated forest and mature forest. However, snapped stems were significantly more abundant in the disturbed forests than in the mature forest. Although snapping was not fatal, it definitely retarded tree growth. Furthermore, multiple snapping was observed in disturbed forests only. It therefore appears that, impaired recruitment of juveniles into the adult size class, is the major cause of slow regeneration of *Strombosia* in the disturbed forests.

In terms of management, it appears that mechanical logging and elephant conservation will be difficult to achieve in the same forest, unless logging techniques that minimize gap sizes are employed. The regeneration in compartments that were logged over 25 years ago, does not appear as if it will warrant a second felling within the 70 year cycle anticipated in the management plan (Osmaston 1959). Elephants are partially responsible for the slow regeneration. Because many of the tree species selected by elephants are timber species (Wing & Buss 1970), it is unlikely that heavily logged forests can attain original stocking densities of commercial species in a 70 year cycle. There is a need to study the relationship between gap density and size, and frequency of use by elephants. This may help in the formulation of logging practices that

minimize subsequent elephant damage. Also, the herbaceous
tangle itself physically suppresses and competes for light
and nutrients with seedlings and saplings.

Summary of Major Points

1) Survival of control seeds of *Strombosia* and
seedlings was higher in the logged forest than in the mature
forest.

2) Survival of control seeds of *Mimusops* and seedlings
did not differ between mature and logged forest.

3) In the mature forest, survival of control seeds and
of seedlings did not differ between gaps and understory.
Strombosia seeds in phase 2 were an exception in that the
control seeds survived longer in the understory than in
gaps.

4) In the second phase experiment, control seeds of
Mimusops and *Strombosia* in the logged forest, survived
longer in the understory than in gaps.

5) Exclusion of large mammals did not increase seed
survival.

6) Seeds in rodent exclosures survived longer than
control seeds for both *Mimusops* and *Strombosia*.

7) In the mature forest, when rodents were excluded,
more seeds of *Mimusops* became established seedlings in gaps
than in the understory. In the logged forest, the number of
Mimusops seeds that became established seedlings in gaps and
in the understory were equal when rodents were excluded.

For *Strombosia*, the number of seeds that became established seedlings when rodents were excluded, did not differ among gaps and understories of logged and mature forests.

8) The rodent population in the logged and in mature forests were unusually high during this study.

9) The number of unique individuals and trap success, unlike in previous studies (Isabirye-Basuta 1979, Kasenene 1984, Isabirye-Basuta & Kasenene 1987, Muganga 1989), were unusually higher in the mature forest than in the logged forest.

10) A higher proportion of *Mimusops* and *Strombosia* trees < 10 cm dbh were damaged by elephants in the disturbed forests than in the mature forest.

Conclusions

1) *Strombosia* seed and seedling survival were low where rodent abundance was high (mature forest) and were high where rodent abundance was low (logged forest). It was therefore concluded that seed and seedling survival, are influenced by rodent abundance.

2) Seed and seedling survival in gaps and understory is not only influenced by rodent abundance, and habitat type (gap or understory), but also by subtle characteristics such as litter depth. Such characteristics were shown to vary between forest types.

3) The frequent browsing on juvenile trees by elephants contributes to the slow regeneration of trees in logged forests. Therefore, selective logging may not be sustainable in forests that are inhabited by elephants unless the logging practices are improved considerably.

Table A.1: Estimates of habitat variables, canopy openness, ground vegetation cover, litter depth, and volume of fallen wood, at seed/seedling stations in gaps and understories of mature and logged compartments of Kibale Forest Reserve.

Habitat type	Station	Habitat variables			
		Canopy openness	Ground vegetation cover (%)	Litter depth (cm)	Volume of wood (m^3)
Mature forest gaps	01	10.0	080	1.20	00.0
	02	09.0	037	2.00	24.0
	03	03.0	065	0.10	00.5
	04	08.0	057	1.00	01.2
	05	15.0	028	1.00	00.0
	06	16.0	093	1.50	00.0
	07	13.0	016	0.55	00.5
	08	06.0	012	1.25	00.1
	09	04.0	028	0.50	00.8
	10	13.0	022	5.00	00.2
	11	14.0	033	1.00	06.7
	12	07.0	029	0.30	01.2
	13	15.0	074	0.80	05.6
	14	06.0	011	2.00	01.0
	15	05.0	012	2.80	18.4
	16	16.0	065	1.30	03.6
	17	08.0	052	1.30	01.6
	18	05.0	086	1.30	07.0
	19	16.0	045	0.10	00.0
	20	09.0	031	1.50	00.0
	21	04.0	013	1.30	12.5
	22	03.0	009	1.30	08.0
	23	03.0	002	2.00	07.0
	24	06.0	013	3.50	06.7
	25	03.0	015	1.50	00.4
	26	09.0	081	0.75	03.7
	27	06.0	075	1.30	00.0
	28	10.0	075	0.10	00.0
	29	16.0	090	1.50	00.0
	30	12.0	095	2.00	00.0
Mature forest understory	01	01.0	006	1.30	02.5
	02	01.0	013	2.40	00.0
	03	00.5	019	1.30	00.0
	04	01.5	022	1.20	01.5
	05	00.5	002	2.50	00.3
	06	00.5	005	1.80	00.0

Table A.1 -- continued

| Habitat type | Station | Habitat variables | | | |
		Canopy openness	Ground vegetation cover (%)	Litter depth (cm)	Volume of wood (m^3)
Mature forest understory	07	00.5	005	2.20	00.0
	08	01.5	026	0.80	00.5
	09	00.5	031	1.70	00.0
	10	00.5	013	1.00	00.4
	11	01.0	004	1.30	00.0
	12	01.0	004	1.70	00.0
	13	01.5	008	1.00	00.0
	14	00.5	002	1.20	01.2
	15	02.0	034	0.50	01.2
	16	01.0	020	1.50	00.0
	17	01.0	012	1.50	00.0
	18	00.5	022	0.70	00.0
	19	01.0	019	1.30	01.6
	20	00.5	003	1.70	00.0
	21	02.0	001	1.70	02.0
	22	01.0	005	2.20	04.0
	23	01.5	004	2.30	00.0
	24	02.0	006	1.30	00.2
	25	01.0	002	1.00	00.5
	26	02.0	022	1.70	01.2
	27	00.5	043	1.20	00.0
	28	01.0	007	1.50	00.0
	29	02.5	005	1.20	00.3
	30	00.5	016	2.00	00.0
Logged forest gaps	01	14.0	077	1.70	00.0
	02	16.0	098	0.80	00.0
	03	14.0	042	1.30	00.0
	04	13.0	090	1.40	00.0
	05	07.0	062	2.10	00.0
	06	06.0	074	2.30	00.0
	07	11.0	086	1.00	00.0
	08	16.0	096	1.10	00.0
	09	16.0	097	1.10	00.0
	10	13.0	089	1.00	00.0
	11	09.0	092	1.80	00.0
	12	11.0	100	1.40	00.0
	13	16.0	090	1.25	00.0
	14	00.5	013	0.50	01.3
	15	07.0	062	1.40	00.0
	16	07.0	059	0.90	00.0
	17	15.0	100	1.63	00.0
	18	16.0	100	1.40	00.0
	19	11.0	091	2.30	00.0
	20	16.0	100	1.38	00.0
	21	16.0	100	1.88	00.0
	22	13.0	095	1.00	00.0

Table A.1 -- continued

		Habitat variables			
Habitat type	Station	Canopy openness	Ground vegetation cover (%)	Litter depth (cm)	Volume of wood (m^3)
Logged forest	23	15.0	099	1.13	00.0
gaps	24	07.0	079	0.63	00.0
	25	04.0	055	1.00	00.0
	26	10.0	091	0.75	00.0
	27	14.0	089	1.00	00.5
	28	15.0	099	2.00	01.3
	29	16.0	100	2.00	00.0
	30	14.0	094	0.75	00.0
Logged forest	01	01.0	003	0.50	06.2
understory	02	01.5	012	2.10	00.0
	03	01.3	005	2.00	00.0
	04	01.0	009	1.70	01.3
	05	00.5	002	2.30	00.0
	06	01.5	023	2.00	00.4
	07	00.5	008	3.00	00.0
	08	00.5	001	3.80	02.5
	09	01.5	002	2.75	00.5
	10	01.0	001	2.50	00.0
	11	01.5	007	2.50	05.3
	12	01.0	001	1.50	04.3
	13	02.0	022	3.70	00.5
	14	03.0	003	2.20	01.3
	15	01.5	003	2.00	00.0
	16	02.5	007	1.80	00.2
	17	01.0	008	1.75	00.0
	18	03.0	008	2.50	00.0
	19	02.0	003	1.30	00.0
	20	03.0	013	1.25	01.7
	21	01.5	008	2.00	04.1
	22	01.0	013	2.75	00.3
	23	03.0	013	1.80	00.0
	24	00.5	008	1.80	00.5
	25	01.0	003	1.70	00.3
	26	03.0	008	2.00	00.0
	27	02.0	014	1.80	00.8
	28	03.0	019	2.00	03.2
	29	01.0	005	1.50	00.0
	30	02.0	010	1.00	00.0

Table A.2: Number of days survived by Mimusops and
Strombosia (study phase one) seeds in gaps and understories
of mature and logged forest compartments of Kibale Forest
Reserve. Columns A, B, and C represent, control, large
mammal exclosure and rodent exclosure treatments,
respectively.

Habitat types

		Mature forest gaps			Mature forest under-story			Logged forest gaps			Logged forest under-story		
		Number of days survived												
Seed species	Station	A	B	C	A	B	C	A	B	C	A	B	C
Mimusops	01	35	02	87	02	35	87	05	05	87	05	35	87
	02	35	25	87	35	01	87	20	09	87	17	07	87
	03	10	42	87	12	56	87	07	07	87	35	01	87
	04	25	06	87	35	12	87	09	09	87	01	07	87
	05	06	10	03	12	42	24	24	17	87	25	87	87
	06	10	10	11	01	01	01	01	01	87	63	53	87
	07	25	10	87	10	25	15	07	07	87	07	87	87
	08	14	06	49	10	06	56	11	03	42	11	49	87
	09	10	04	87	10	06	56	07	56	63	77	35	56
	10	48	02	87	06	12	87	87	56	87	70	35	87
	11	25	25	13	01	25	87	05	01	87	25	42	87
	12	35	35	87	01	16	87	11	01	87	11	87	77
	13	04	04	87	02	10	87	01	07	42	01	01	87
	14	01	02	87	04	06	87	07	07	87	42	25	87
	15	35	42	56	12	25	77	25	07	87	25	87	49
	16	10	49	87	10	08	87	07	13	87	01	03	87
	17	10	87	87	10	16	87	25	07	87	07	09	87
	18	01	08	87	10	10	49	25	01	87	09	13	87
	19	14	77	87	49	49	87	87	42	87	25	25	87
	20	56	16	87	14	10	87	07	35	87	03	03	87
	21	87	01	87	02	70	87	03	01	87	87	07	87
	22	08	08	09	06	06	87	03	01	07	05	17	87
	23	56	49	87	02	04	87	49	09	87	03	25	87
	24	04	10	87	77	87	87	01	25	87	42	35	56
	25	49	70	87	02	06	87	56	03	24	25	09	87
	26	06	06	11	87	49	87	13	35	87	11	01	24
	27	77	87	87	77	06	87	09	35	56	35	01	87
	28	87	25	87	42	56	56	49	77	87	87	49	87
	29	25	01	87	25	42	87	25	03	87	01	05	87
	30	04	01	87	25	02	87	11	11	87	35	25	15
Strombosia	01	25	04	87	02	87	87	34	18	87	32	35	87
	02	06	19	87	65	04	87	03	87	87	87	87	87
	03	41	87	87	11	01	87	26	13	87	87	87	87
	04	04	87	87	25	04	87	87	12	87	87	01	87
	05	04	10	03	40	02	19	87	25	87	87	87	87
	06	69	04	11	40	04	01	03	01	87	32	63	87

Table A.2 -- continued

Habitat types

		Mature forest gaps			Mature forest under- story			Logged forest gaps			Logged forest under- story		
		Number of days survived												
Strombosia	07	02	01	87	44	08	56	87	56	87	34	87	87
	08	08	01	05	38	01	56	03	87	87	87	87	87
	09	50	20	87	25	04	56	09	25	70	03	10	87
	10	04	01	87	25	34	87	05	42	87	87	87	87
	11	32	01	13	13	01	11	03	06	87	34	87	87
	12	02	20	56	13	01	87	05	25	87	34	87	87
	13	19	04	87	44	08	87	07	10	87	38	06	87
	14	02	06	87	52	06	87	05	49	87	36	87	87
	15	02	87	56	04	56	87	07	16	87	05	01	49
	16	11	04	87	04	14	87	11	87	87	38	01	87
	17	25	44	87	02	31	87	24	14	87	34	25	87
	18	02	50	87	25	87	87	29	06	87	34	25	87
	19	11	01	87	13	56	87	33	08	87	36	25	87
	20	87	87	87	56	31	87	11	87	87	03	08	87
	21	39	16	87	04	87	87	17	25	87	34	87	87
	22	04	87	87	07	87	87	05	16	87	05	16	87
	23	87	10	87	02	08	87	24	01	87	54	87	87
	24	11	02	87	87	87	87	05	02	87	87	06	56
	25	11	36	87	42	06	87	63	06	87	36	25	87
	26	05	06	11	02	01	87	24	25	87	63	12	42
	27	02	08	87	25	35	87	84	02	87	87	56	87
	28	07	04	87	64	01	35	63	10	87	44	16	87
	29	44	02	09	42	42	87	87	14	87	87	87	87
	30	44	01	87	02	35	87	05	14	87	03	87	87

Table A.3: Number of days survived by *Mimusops* and
Strombosia (study phase two) seeds in gaps and understories
of mature and logged forest compartments of Kibale Forest
Reserve. Columns A, B, and C represent, control, large
mammal exclosure and rodent exclosure treatments,
respectively.

Habitat types

Seed species	Station	Mature forest gaps			Mature forest under-story			Logged forest gaps			Logged forest under-story		
		A	B	C	A	B	C	A	B	C	A	B	C
						Number of days survived								
Mimusops	01	29	01	95	01	05	29	22	15	95	29	22	95
	02	05	50	95	95	36	95	78	64	78	95	92	95
	03	95	78	95	71	01	95	22	22	95	95	95	95
	04	07	01	95	07	01	95	71	92	95	01	05	64
	05	07	01	78	95	64	95	05	09	95	95	95	95
	06	01	29	95	78	09	95	01	03	95	95	70	95
	07	09	07	78	95	95	95	95	05	95	29	07	95
	08	07	01	71	71	78	95	07	57	95	95	36	95
	09	95	71	95	78	92	95	03	13	03	92	36	95
	10	95	05	95	01	01	95	64	78	95	95	95	01
	11	43	29	95	15	15	95	03	03	95	95	95	95
	12	36	50	95	03	92	85	64	29	95	78	95	95
	13	71	71	95	50	95	95	11	03	95	15	29	95
	14	01	03	95	71	43	64	43	17	95	07	29	95
	15	95	78	95	71	43	15	01	09	95	03	95	95
	16	95	22	95	22	22	95	64	43	29	95	95	95
	17	70	57	95	64	17	95	29	01	95	09	95	95
	18	01	22	95	01	01	95	05	11	95	29	13	95
	19	95	71	95	43	64	95	43	57	95	95	95	95
	20	29	29	95	29	05	95	11	01	95	57	71	95
	21	36	29	71	09	17	95	36	01	78	95	85	85
	22	71	95	95	64	71	95	01	03	95	50	11	95
	23	11	29	95	64	95	95	03	22	95	64	85	95
	24	22	01	95	07	78	95	29	05	95	95	95	95
	25	95	22	95	01	95	95	95	43	95	95	29	95
	26	95	01	95	09	01	95	20	05	71	95	43	95
	27	92	13	95	95	13	95	95	09	95	01	95	09
	28	71	43	71	95	09	95	71	07	95	09	95	95
	29	07	03	95	78	78	95	01	01	95	85	78	95
	30	36	22	71	71	22	71	64	11	95	95	95	50
Strombosia	01	01	29	50	11	43	42	22	22	29	29	95	95
	02	43	78	95	57	95	95	29	07	95	64	64	95
	03	43	22	95	64	22	57	50	85	95	95	95	95
	04	57	95	95	92	95	95	95	95	57	64	85	95
	05	85	01	95	57	57	95	22	57	95	71	27	95
	06	22	22	95	95	95	92	29	57	95	95	43	95

Table A.3 -- continued

		Mature forest gaps			Mature forest under-story			Logged forest gaps			Logged forest under-story		

		Number of days survived												
Strombosia	07	01	29	78	43	71	95	92	22	95	64	43	95
	08	64	07	64	85	71	95	71	01	78	95	95	64
	09	29	29	95	29	09	95	64	15	95	95	95	95
	10	64	22	95	09	05	95	57	01	95	95	64	95
	11	71	29	95	43	11	95	36	36	95	95	78	95
	12	17	64	50	71	05	95	01	29	95	78	95	95
	13	43	57	95	64	85	71	07	29	95	95	71	95
	14	92	29	95	57	50	95	36	95	95	78	29	95
	15	01	78	95	95	29	64	71	64	95	95	64	95
	16	01	22	95	05	71	92	29	01	29	95	95	95
	17	07	71	95	71	36	50	29	36	43	78	29	95
	18	15	01	95	78	64	95	05	85	95	95	95	95
	19	22	11	95	71	22	95	03	03	95	43	95	95
	20	29	29	95	29	50	29	43	11	95	95	71	57
	21	57	13	95	95	71	85	01	43	64	92	71	57
	22	57	17	29	71	78	95	03	01	95	64	01	71
	23	03	01	95	50	78	50	17	64	95	95	17	22
	24	03	13	95	22	15	95	17	78	95	95	05	95
	25	05	95	95	43	95	43	01	95	95	78	71	29
	26	15	17	95	07	15	95	01	78	95	95	09	71
	27	01	50	95	09	03	09	78	29	95	78	95	71
	28	03	78	71	43	71	95	95	01	95	95	95	95
	29	03	22	95	11	95	95	09	29	95	95	95	95
	30	71	57	95	11	57	95	13	29	95	95	85	50

Table A.4: Average number of days (indicating ranges and
standard deviations) survived by *Mimusops* phase one seeds in
gaps and understories of mature and logged forests.

Average duration (days)

Habitat type	Control	Large Mammal Exclosures	Rodent Exclosures
Mature forest gap	26.76 ± 25.4 (1-87)	22.96 ± 26.1 (1-87)	71.76 ± 29.1 (3-87)
Mature forest understory	19.7 ± 24.2 (1-87)	23.06 ± 22.7 (1-87)	74.93 ± 23.9 (1-87)
Logged forest gap	19.9 ± 23.3 (1-87)	16.3 ± 19.9 1-87)	77.4 ± 21.3 (7-87)
Logged forest understory	26.7 + 26.3 (1-87)	28.8 + 28.1 (1-87)	78.8 + 19.1 (15-87)

Table A.5: Average number of days (indicating ranges and
standard deviations) survived by *Mimusops* phase two seeds in
gaps and understories of mature and logged forests.

Average duration (days)

Habitat type	Control	Large Mammal Exclosures	Rodent Exclosures
Mature forest gap	47.4 ± 37.8 (1-95)	30.86 ± 28.7 (1-95)	90.6 ± 8.9 (71-95)
Mature forest understory	48.46 ± 35.5 (1-95)	41.93 ± 36.6 (1-95)	87.96 ± 19.3 (15-95)
Logged forest gap	35.2 ± 32.5 (1-95)	21.3 ± 25.1 (1-92)	87.8 ± 20.6 (3-95)
Logged forest understory	62.93 + 38.1 (1-95)	65.8 + 34.2 (5-95)	86.13 + 24.1 (1-95)

Table A.6: Average number of days (indicating ranges and standard deviations) survived by *Strombosia* phase one seeds in gaps and understories of mature and logged forests.

Average duration (days)

Habitat type	Control	Large Mammal Exclosures	Rodent Exclosures
Mature forest gap	20.86 ± 24.9 (2-87)	23.66 ± 31.4 (1-87)	69.26 ± 31.8 (3-87)
Mature forest understory	27.16 ± 23.1 (1-87)	27.63 ± 31.6 (1-87)	71.8 ± 28.1 (1-87)
Logged forest gap	28.5 ± 30.6 (3-87)	26.3 ± 27.6 (1-87)	86.5 ± 3.1 (70-87)
Logged forest understory	47.16 ± 29.9 (3-87)	48.7 ± 36.6 (1-87)	83.2 ± 11.7 (42-87)

Table A.7: Average number of days (indicating ranges and standard deviations) survived by *Strombosia* phase two seeds in gaps and understories of mature and logged forests.

Average duration (days)

Habitat type	Control	Large Mammal Exclosures	Rodent Exclosures
Mature forest gap	30.8 ± 28.9 (1-92)	36.2 ± 28.4 (1-95)	87.4 ± 17.1 (29-95)
Mature forest understory	49.6 ± 29.8 (5-95)	52.0 ± 31.7 (3-95)	78.6 ± 24.2 (9-95)
Logged forest gap	34.2 ± 30.5 (1-95)	43.7 ± 34.2 (1-95)	85.8 ± 20.7 (23-95)
Logged forest understory	83.2 ± 17.4 (29-95)	66.6 ± 32.1 (1-95)	82.9 ± 21.1 (22-95)

Table A.8: Number of days survived by *Mimusops* and *Strombosia* seedlings in gaps and understories of mature and logged forest compartments of Kibale Forest Reserve. Columns A and B represent number of days survived prior to non fatal and fatal stem damage respectively.

Seedling species	Station	Mature forest gaps		Mature forest under-story		Logged forest gaps		Logged forest under-story	
		A	B	A	B	A	B	A	B
		Number of days survived							
Mimusops	01	---	062	---	062	---	122	---	122
	02	---	017	---	025	---	051	---	122
	03	---	048	---	062	---	059	---	122
	04	---	062	---	062	---	017	---	122
	05	---	062	---	007	---	077	---	054
	06	---	007	---	007	---	044	---	122
	07	---	034	---	062	---	122	---	031
	08	---	062	---	062	---	011	---	122
	09	---	062	---	007	---	044	---	024
	10	---	025	---	062	---	122	---	122
	11	---	025	---	048	---	003	---	122
	12	---	031	---	062	---	011	---	122
	13	---	062	---	007	---	011	---	122
	14	---	062	---	062	---	011	---	059
	15	---	062	---	007	---	122	---	122
	16	---	062	---	007	---	038	---	122
	17	---	062	---	062	---	017	---	003
	18	---	062	---	062	---	122	---	122
	19	---	007	---	017	---	122	---	122
	20	---	062	---	062	---	122	---	122
	21	---	062	---	062	---	017	---	122
	22	---	062	---	062	---	003	---	122
	23	---	062	---	062	---	122	---	122
	24	---	062	---	007	---	122	---	122
	25	---	062	---	062	---	017	---	122
	26	---	062	---	062	---	003	---	122
	27	---	062	---	062	---	011	---	122
	28	---	031	---	062	---	122	---	122
	29	---	062	---	062	---	011	---	122
	30	---	062	---	062	---	122	---	122
Strombosia	01	003	025	025	122	122	122	031	122
	02	025	122	122	122	122	122	051	122
	03	025	032	077	122	122	122	122	122
	04	003	122	025	122	038	122	011	024
	05	003	051	017	017	077	122	024	122
	06	017	017	122	122	018	024	122	122
	07	003	003	003	011	122	122	122	122
	08	003	038	011	044	077	122	122	122

Table A.8 -- continued

Seedling species	Station	Mature forest gaps		Mature forest under- story		Logged forest gaps		Logged forest under- story	
		A	B	A	B	A	B	A	B
				Number of days survived					
Strombosia	09	011	122	003	003	122	122	059	059
	10	122	122	122	122	077	077	122	122
	11	003	025	077	122	025	122	051	122
	12	003	003	003	003	077	122	122	122
	13	003	003	003	122	011	031	011	122
	14	003	003	038	077	003	122	122	122
	15	122	122	059	122	003	122	038	122
	16	011	122	003	003	003	044	122	122
	17	051	122	018	038	122	122	122	122
	18	077	122	011	122	031	122	122	122
	19	003	077	003	122	077	122	051	077
	20	003	003	122	122	031	122	077	122
	21	032	122	059	122	051	077	031	122
	22	059	059	003	077	003	038	122	122
	23	003	038	122	122	122	122	122	122
	24	003	003	059	077	024	122	122	122
	25	032	122	003	025	038	038	051	122
	26	025	032	003	003	003	024	024	024
	27	038	038	011	011	038	122	122	122
	28	003	003	003	011	122	122	051	122
	29	011	011	003	003	077	122	051	122
	30	003	003	003	003	011	122	122	122

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BIOGRAPHICAL SKETCH

Jeremiah Ssali Lwanga was born and raised in Uganda. Jeremiah received his B. Sc. and M. Sc. at Makerere University, Uganda in 1984, and 1989, respectively. His M. Sc. thesis focused on the socioecology of blue monkeys in the Kibale Forest Reserve. In 1988, Jeremiah enrolled at University of Florida as a post-baccalaureate student in the Department of Wildlife and Range Sciences, and in 1990, he was accepted as a doctoral student in the same department.

I certify that I have read this study and that in my
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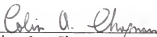as a dissertation for the degree of Doctor of Philosophy.

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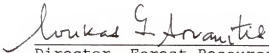Assistant Professor of Botany

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